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Paleoecological Analysis of theVertebrate Fauna of the Morrison Formation (Upper Jurassic), Rocky Mountain Region, U.S.A.

by

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New Mexico Museum of Natural History & Science

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Cover illustration: Restoration of the sauropod dinosaur *Camarasaurus*, most common sauropod of the Morrison Formation. By Dan Varner, 1993.

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Frontispiece: A scene from western Colorado during Morrison time. An *Allosaurus* attempts to take over a sauropod carcass from two *Ceratosaurus*. In the background, across a pond lined with horsetails and sauropod bones, an *Apatosaurus* and a *Mymoorapelta* take a drink. Based on work at the Mygatt-Moore Quarry, Mesa County, Colorado. Illustration courtesy of Pat Redman.

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PALEOECOLOGICAL ANALYSIS OF THE VERTEBRATE FAUNA OF THE MORRISON FORMATION (UPPER JURASSIC), ROCKY MOUNTAIN REGION, U.S.A.

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Abstract–The Morrison Formation is well known for its diverse assemblage of fossil vertebrates. Diversities, relative abundances, and biomasses of taxa and ecological guilds of the diverse vertebrate paleofauna from this unit were analyzed for variation by stratigraphic level, geographic region, and paleoenvironmental context. Counts of the numbers of specimens of each taxon from more than 200 sites were compiled in order to determine the relative abundances. Within a range of expected variation due to different sample sizes and diversities preserved at certain large quarries, the structure of the paleocommunities in the Morrison Formation appears to have been fairly consistent during at least the last 4-6 my, and possibly all of the approximately 8 my of deposition. The diversity of Morrison vertebrate taxa was relatively high and consistent throughout deposition. As nearly as can be determined from death assemblages, the Morrison Formation paleocommunity was different from any modern community and most ancient ones in having a relatively high abundance and diversity of very large vertebrate animals.

Vertebrate biomass appears to have been dominated by large herbivores to an even greater degree than are modern megaherbivore community biomasses, and this may have had an indirect impact on the abundances and diversities of smaller herbivores, small predators, and small non-dinosaurian reptiles. The abundance of microvertebrates in the formation appears to have been reasonably high and may indicate moderately high plant productivity and habitat heterogeneity.

In addition to the sauropods, the most common and ecologically important dinosaurs included the ornithopods and the theropod *Allosaurus*.

A paucity of vertebrate prey species in the middle adult weight categories (10-500 kg) may have been caused by competitive pressure from juveniles of larger dinosaur species, as well as possibly selective pressure from predators in the middle to large size ranges.

The long-ranging non-dinosaurian taxa may have been relatively more abundant in the upper part of the formation and maintained higher diversities than the long-ranging dinosaurs. Thus, dinosaur diversity may have dropped slightly relative to non-dinosaurs near the end of Morrison deposition.
Keywords: Upper Jurassic, Morrison Formation, paleoecology, paleoenvironment, diversity

INTRODUCTION

The Morrison Formation is an extensive deposit of predominantly continental sedimentary rocks of Late Jurassic age that is exposed throughout much of the Rocky Mountain region of the western United States. A diverse collection of vertebrate fossils is known from the formation and forms a large database with which to study the paleoecology of the Morrison Formation vertebrate fauna. The fossil vertebrates in the formation represent a variety of animals that presumably lived across a range of environments and geographic areas. Through time, these associations and the relative abundances of the animals likely changed. Some animals were probably wide-ranging geographically and environmentally, and others were likely more restricted. The animals living in particular times, areas, or environments formed paleocommunities, and these communities were characterized by the structure of the paleoecological roles of the component taxa. The aim of the present study is to determine what changes in vertebrate paleocommunities occurred during deposition of the Morrison Formation through time and between various paleoenvironments, as well as what these changes indicate for the evolution and variation of vertebrate paleoecological associations during the Late Jurassic in western North America.

Dodson et al. (1980) studied the taphonomy and generalized paleoecology of the formation, but concluded that a quantitative faunal analysis would only be possible once more information was available. Dale Russell (1989 and in Coe et al., 1987) was able to estimate the relative population percentages of the community formed by Morrison Formation dinosaur genera based on an unpublished census of dinosaur collections and using a calculation developed by Behrensmeyer et al. (1979). In the past few years, a significant amount of additional information has become available on new and old sites as a result of renewed interest in both dinosaurs in general and the Morrison Formation in particular. It should now be possible to test Russell's population percentages with a more up-to-date census that also includes non-dinosaurian taxa. From these population reconstructions and estimations of the ecological roles of each taxon, it should be possible to determine any changes in the paleoecological structure of the Morrison vertebrate communities through time, across geographic ranges, and from one subenvironment to another. With a complete survey of the numbers and types of animals preserved from many quarries throughout the Morrison, it will be feasible to compare the distributions of species within this ancient Jurassic paleocommunity.

History

Outcrops of the Morrison Formation are present in Utah, Colorado, Wyoming, Montana, and New Mexico, as well as north-

eastern Arizona, the western end of the Oklahoma Panhandle, and western South Dakota. In addition, the Morrison Formation is present in the subsurface below western Kansas, Nebraska, and North Dakota, and below the northwestern Texas Panhandle (Fig. 1). The formation was first named by Cross (1894) for exposures near the town of Morrison, Colorado, and later described more thoroughly by Eldridge (1896). Prior to this, O.C. Marsh had referred to the thick mudstone unit in the middle of the formation as the "*Atlantosaurus* Beds" in his reports on the vertebrate fauna that were published during the late 1800s.

The first work in the Morrison Formation was paleontological, as remains of dinosaurs were found in this unit in the second half of the nineteenth century. The first remains of dinosaurs were probably collected in 1859 by John Newberry from what is now southeastern Utah (Gillette, 1996a,b) and named by E. D. Cope as *Dystrophaeus viaemalae* (Cope, 1877c). The first major discoveries were at Morrison and at Garden Park north of Cañon City, both along the Front Range of Colorado, and at Como Bluff, Wyoming, all in 1877 (Ostrom and McIntosh, 1966; Colbert, 1968; Kohl and McIntosh, 1997; Monaco, 1998). More quarries were soon found throughout the region including those in the Grand Valley of western Colorado, along the northern edge of the Uncompahgre Plateau; in the Sheep Creek area in south-central Wyoming; south of the Uinta Mountains near Jensen, Utah, which became the Carnegie Quarry of Dinosaur National Monument; at Dry Mesa in western Colorado; on the Howe Ranch along the Bighorn Mountains in north-central Wyoming; and in the San Rafael Swell in central Utah (Cleveland-Lloyd Quarry). The number of known dinosaur taxa soon became quite large and has continued to grow. By the 1950s, most of the geologic work in the Morrison Formation was concentrated on locating uranium and vanadium deposits (e.g. Carter and Gualtieri, 1965), but even this was productive paleontologically, as at least two known vertebrate tracksites in the formation are in uranium mines (Foster and Lockley, 1997; Lockley et al., 1998).

Morrison Formation Geology

The Morrison Formation is exposed around the edges of uplifted areas in the Rocky Mountain region of the western states; exposures are found on the flanks of the San Rafael Swell in Utah, the Black Hills in South Dakota and Wyoming, the Bighorn Mountains in Wyoming, and the Uncompahgre Uplift and the Front Range in Colorado. In most areas, the Morrison Formation overlies Middle and Upper Jurassic marine units, including the Sundance Formation in the north and northeast and the Summerville-Wanakah formations in the Colorado Plateau. Overlying the Morrison Formation are a variety of Lower Cretaceous formations, including the Cloverly Formation in northern regions, the Cedar Mountain or Burro Canyon Formations in the western Colorado Plateau outcrop areas, the Lakota Formation in the Black Hills, and the Dakota Group in much of eastern Colorado and eastern New Mexico.

The Morrison Formation is up to several hundred meters thick in the southwestern areas, ~200 m thick near Dinosaur National Monument (Bilbey et al., 1974), and as thin as 25 m in the northeast. The unit is characterized by interbedded tan and white sandstones; green, gray, and red mudstones; and gray limestones.

Members

In the southern Colorado Plateau region, the Morrison Formation has been divided into as many as nine members, although nowhere do all of these members occur in single area. Generally, more members are recognized at localities in the Colorado Plateau region than at localities farther north, where members are often not even defined. The members proposed on the Colorado

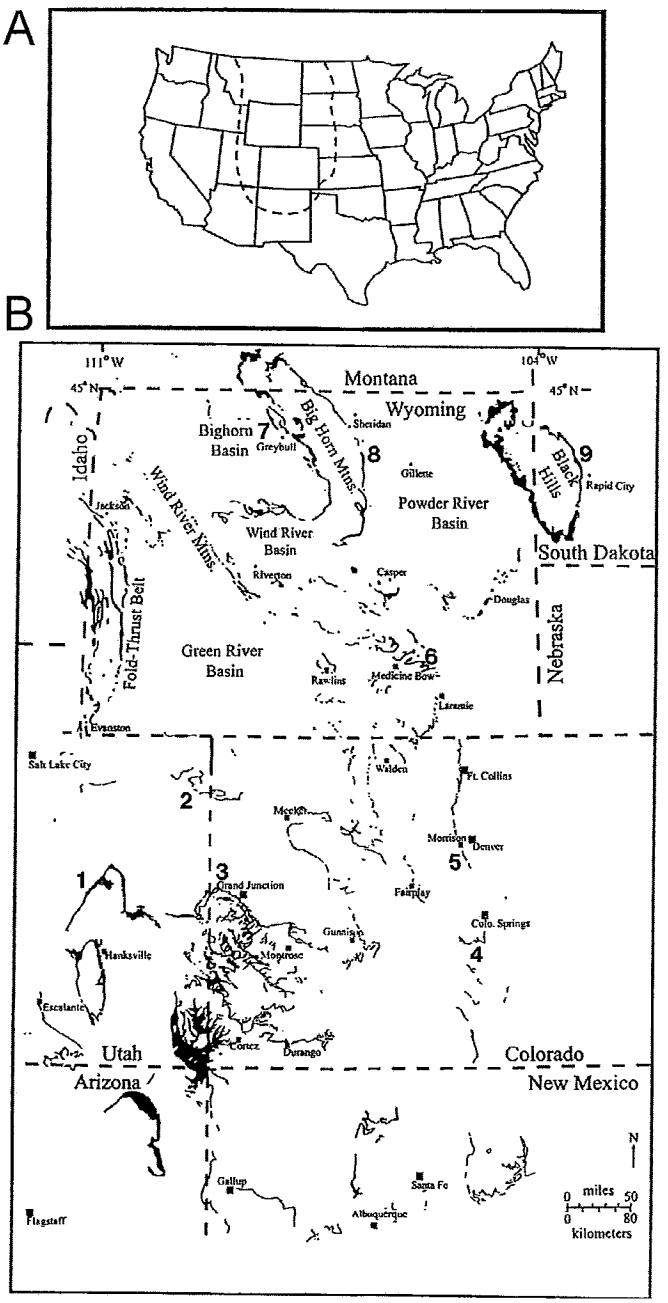

FIGURE 1. (A) Distribution of the Morrison Formation in the Rocky Mountain region of the western United States. Dashed line indicates extent of the formation in outcrop and subsurface. (B) Locations of some quarry areas in relation to outcrop distribution of the Morrison Formation, exclusive of some areas in central Montana and western Oklahoma. Outcrop pattern on map includes overlying Lower Cretaceous formations in some areas, as well as Upper Jurassic–Lower Cretaceous Gannett Group rocks in Idaho and far western Wyoming. Numbered areas and selected quarries include: (1) San Rafael Swell, Cleveland-Lloyd Quarry; (2) Dinosaur National Monument, Carnegie Quarry and Rainbow Park; (3) northern Uncompahgre Plateau, Mygatt-Moore Quarry and Fruita Paleontological Area; (4) Garden Park, Marsh-Felch Quarry and Cope Quarries; (5) Morrison Hogback, Lakes Quarries; (6) Como Bluff and vicinity, Quarry 9, Quarry 13, and Bone Cabin Quarry; (7), Shell area, Howe Quarry; (8) Buffalo area, Poison Creek Quarry; (9) eastern Black Hills, Wonderland Quarry. Outcrop map by K. Trujillo, based on Craig et al. (1955) and Zaleha et al. (2001).

Plateau include the Tidwell, Bluff Sandstone, Salt Wash, Recapture, Westwater Canyon, Brushy Basin, Fiftymile, and Jackpile Sandstone members (Peterson and Turner-Peterson, 1987; Condon and Huffman, 1988; Peterson 1988). Anderson and Lucas (1995, 1996) only recognized the Salt Wash, Brushy Basin, Fiftymile and Jackpile members as part of the Morrison and indicated that some proposed members belonged in underlying formations or were part of the Salt Wash or Brushy Basin. Several of the named members from the southern Colorado Plateau are laterally restricted and almost all of them grade into other members at one place or another (Fig. 2; alternative stratigraphy of Anderson and Lucas in Fig. 3). In the northern Colorado Plateau region, the defined members are, in ascending order, the Windy Hill, Tidwell, Salt Wash, and Brushy Basin members. These are also the geographically most widely recognized members in the formation, extending into northeastern Utah and west-central Colorado. The Windy Hill of northern outcrops is included by some in the Sundance Formation (Imlay, 1980).

Outcrops along the Front Range of Colorado and in Wyoming have not traditionally had recognized members, although Allen (1996) proposed three members for the Morrison Formation in southern Wyoming. These members have not been generally recognized because specific type sections were not established. In ascending order these members are the Lake Como, Talking Rocks, and Indian Fort members. These members were applied mainly to outcrops in the vicinity of Como Bluff (Allen, 1996; Bakker, 1996). Additionally, the Unkpapa Sandstone, an eolian unit that underlies the Morrison in the southern and eastern Black Hills in South Dakota, has been proposed as a member of the Morrison Formation in that region (Szigeti and Fox, 1981). The nine commonly recognized members from the Colorado Plateau are:

Windy Hill Member—The Windy Hill is a mostly northern member that was originally described as the top member of the Sundance Formation by Pipiringos (1968).

Tidwell Member—The Tidwell Member consists of red and gray mudstone, light brown to gray sandstone, light to dark gray limestone, and white gypsum deposits lying unconformably on Middle Jurassic marine rocks. The member can be up to 82 m thick but is more commonly 8-23 m. These deposits are believed to represent mudflat, freshwater and saline lake, and rare marine, fluvial, and eolian depositional environments (Peterson and Turner-Peterson, 1987; Peterson, 1988). Anderson and Lucas (1995) consider this member a part of the Summerville Formation. One sauropod specimen, several trackways, and a partial pterosaur are the only vertebrate fossils known from this member.

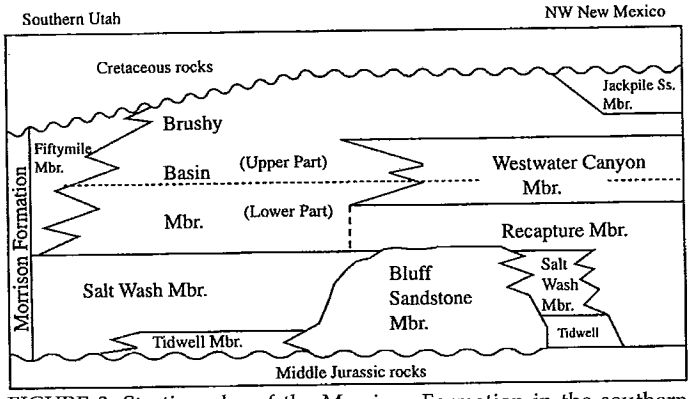

FIGURE 2. Stratigraphy of the Morrison Formation in the southern Colorado Plateau region, based on Peterson and Turner-Peterson (1987).

Bluff Sandstone Member—The Bluff Sandstone Member is mainly found in southeastern Utah and northeastern Arizona. This is predominantly a crossbedded eolian sandstone unit that is thickest near Bluff, Utah, and thins to the north, west, and south. No vertebrate body fossils are known from this member.

Salt Wash Member—The Salt Wash Member consists of cliff-forming, pale grayish brown sandstones and thin units of red or grayish-green mudstones. The unit ranges from 30-100 m in thickness (Stokes, 1944). Tyler and Ethridge (1983) interpreted the Salt Wash Member as representing an alluvial plain system of streams draining northeasterly from a southwestern source. The Salt Wash Member is equivalent to the lower portion of the Recapture Member in the southern Colorado Plateau (Stokes 1944; Craig et al., 1955; Condon and Peterson, 1986). Several fossil vertebrate localities and a number of track sites are known from this member.

Brushy Basin Member—The Brushy Basin Member of the Morrison Formation is one of the most widely recognized members and has smectitic and non-smectitic mudstones varying from red, pink, green, purple, white, and brown, along with interbedded sandstones and thin, lenticular limestones. Derr (1974) recognized several of the interbedded sandstones in the Brushy Basin Member as representing meandering stream point bar complexes. Most fossil vertebrate localities are known from the Brushy Basin or correlative units.

Recapture Member—The Recapture Member was named for 0-107 m of red and greenish-gray mudstone, sandstone, and some limestone that occur at the base of the Morrison Formation in parts of the southern Colorado Plateau (Peterson and Turner-

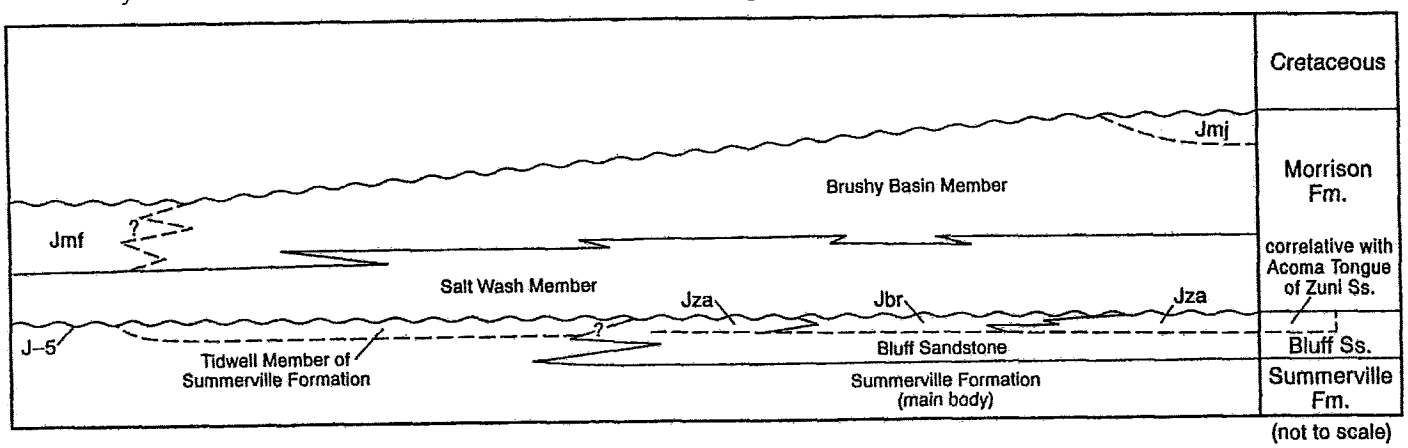

FIGURE 3. Stratigraphy of the Morrison Formation and other units in the southern Colorado Plateau region, from Anderson and Lucas (1995). Jbr = Recapture Member of Bluff Sandstone; Jmf = Fiftymile Member of Morrison Formation; Jmj = Jackpile Member of Morrison Formation; Jza = Acoma Tongue of Zuni Sandstone.

Peterson, 1987). These beds represent fluvial, lacustrine, and eolian paleoenvironments. The sandstones of the Recapture can be distinguished from those of the Salt Wash in that they contain a higher percentage of feldspar and often in larger grain sizes (Cadigan, 1967). Anderson and Lucas (1995, 1996) believed this member is part of the Bluff Sandstone, which they considered a separate formation.

Westwater Canyon Member—The Westwater Canyon Member consists of 0-134 m of cliff-forming, crossbedded sandstone with thin lenses of red or greenish-gray mudstone. The unit probably represents braided stream deposits (Craig et al., 1955), and it is only recognized in the San Juan Basin and Four Corners region. Lithologies of pebbles from this member, as well as paleocurrent analyses, indicate that the Westwater streams drained from source areas to the west and southwest in which igneous, metamorphic, and carbonate rocks were exposed (Turner-Peterson, 1986).

Jackpile Sandstone Member—Owen et al. (1984) named the Jackpile Sandstone Member for crossbedded fluvial sandstones exposed at the top of the Morrison in the southeastern San Juan Basin. Freeman and Hilpert (1956) had already used the Jackpile name informally for the same unit during an earlier uranium survey. The member interfingers with the Brushy Basin Member, and represents the youngest fluvial deposits in the region.

Fiftymile Member—The Fiftymile Member consists of 0-107 m of interbedded sandstone and mudstone in the Straight Cliffs area of southern Utah. The unit is above the steeper and more sandy outcrops of the Salt Wash Member and is laterally equivalent to the Brushy Basin Member (Peterson, 1988).

Age

The age of the Morrison Formation has been discussed at length in the literature since shortly after it was originally named by Cross in 1894, with various arguments proposing a Jurassic, Cretaceous, or Jurassic-Cretaceous age. The various age interpretations were discussed in detail by Kowallis et al. (1998) and need not be discussed further here. Recent isotopic and micropaleontological work, briefly summarized below, clearly indicates a Late Jurassic age for most of the formation.

Sanidine separates from altered volcanic ash beds (now bentonite) and isotopically dated by $^{40}Ar/^{39}Ar$ single-crystal laser-fusion techniques indicate that the formation ranges in age from 147 to 155 Ma (Kowallis et al., 1998). Because the Jurassic ended at about 141 Ma (Bralower et al., 1990), this indicates that the Morrison was deposited during the middle part of the Late Jurassic, a conclusion also suggested by paleomagnetics (Steiner et al., 1994; Steiner, 1998) and by the microfossils. Palynomorphs recovered from the Morrison indicate a Kimmeridgian and early Tithonian age for the formation (Litwin et al., 1998). Spores and pollen from the stratigraphically lowest part of the formation, the Windy Hill Member, suggest a Kimmeridgian age but could, conceivably, be latest Oxfordian in age. Stratigraphically higher parts of the formation have yielded a palynomorph florule clearly indicating a Kimmeridgian age and an early Tithonian age for the highest part of the formation. There are indications, however, that the upper part of the formation in northern regions outside the Colorado Plateau may range into the Early Cretaceous, or that traditionally the boundary between the Morrison and overlying formations in some areas has been placed too high (Trujillo, 2000).

Calcareous microfossils, including charophytes and ostracodes, also indicate a Late Jurassic age for the Morrison (Schudack et al., 1998), although the ages for the lowermost and uppermost strata are not as well defined as was determined from the palynomorphs. Calcareous microfossil samples have not been recovered from the lowest 2-3 m of the formation, but samples from above that stratigraphic position indicate a Kimmeridgian age. The uppermost approximately 30 m have only yielded an assemblage that was somewhat different from lower assemblages but was not clearly indicative of a Tithonian age and so was considered Tithonian(?), based largely on the early Tithonian age determined from palynomorphs (Schudack et al., 1998).

In summary, the Morrison Formation is mostly Kimmeridgian and early Tithonian in age, with the qualifications that the lowermost few meters could possibly be latest Oxfordian in age and that the upper part in some areas may be Early Cretaceous.

Paleoenvironments and Paleoclimates

In most areas, the Morrison Formation is interpreted to consist of continental sediments deposited over much of western North America after the retreat of the Sundance sea during the early Late Jurassic (Stokes, 1944). The source area for these siliciclastic and volcanic sediments was to the west and south (Craig et al., 1955), and this area was probably related to the foreland fold and thrust belt and Andean-type magmatic arc that existed along the western margin of North America at the time (Santos and Turner-Peterson, 1986).

The depositional environments represented by the sedimentary rocks of the Morrison Formation vary greatly from one area to the next, and even the environment of the formation as a whole is sometimes debated. Hatcher (1901) pictured an environment much like the present Amazon basin with abundant tropical vegetation and many rivers and lakes. Similarly, Mook (1915) envisioned an alluvial plain with an interconnected system of rivers, lakes, and swamps with abundant vegetation. Stokes (1944), however, felt that the lakes on the alluvial plain appeared to have been temporary and perhaps seasonal, and that the lack of abundant plant remains in the Morrison Formation and the occurrence of some eolian deposits indicate that semi-desert conditions existed. Moberly (1960) proposed the Gran Chaco Plain of northern Argentina as a modern analog for the Morrison Formation. The Gran Chaco is a vast, 2200 km-long by 1100 km-wide alluvial plain, well-vegetated with patches of forest scattered over savannahs and between lakes and freshwater swamps, with a high average rainfall but with most precipitation in the spring and summer during the rainy season when many areas of the plain become flooded. During the winter dry season, many of the low-lying areas that are under water in the summer become baked mud flats. Dodson et al. (1980) concluded that the Morrison Formation consisted of channel, floodplain, and lacustrine environments and that, though the absence of coals, scarcity of small aquatic vertebrates, abundance of oxidized sediments, and calcretes indicated an occasionally dry environment, plant productivity had to have been high enough to support large herbivores. Craig et al. (1955) cited a greater abundance of plant and dinosaur remains in the upper parts of the Morrison Formation as indicating an increase in humidity.

Among more local studies, Derr (1974), in his study of the sandstones in the Brushy Basin Member, found them to indicate meandering point bar complexes. Based on his discharge calculations he concluded that the area was "hot" and that most plant and animal life was concentrated near streams and lakes. In a study of the Dinosaur Quarry at Dinosaur National Monument in Utah, Lawton (1977) concluded that the sandstones in which the fossils were deposited suggested a braided river with variable discharge. Yen and Reeside (1946) described mollusks from the Morrison Formation in Wyoming that indicated large but shallow bodies of water and fairly dense vegetation. Turner and Fishman (1991) described a large alkaline, saline lake deposit in the Brushy Basin Member of the Morrison Formation from the

Colorado Plateau. They stated that the lake appeared to have been dry more often than it had shallow standing water and that the fluctuations between being exposed and submerged were not seasonal. This indicates an arid to semi-arid climate for the region during deposition of the upper part of the Morrison Formation. Malone and Suttner (1992) described floodplain and fixed channel deposits from the Morrison Formation in Montana that they interpreted to represent a northeast-prograding fan system. Lockley et al. (1986) indicated that much of southeastern Colorado had reasonably large lakes during Morrison time on the basis of freshwater stromatolites, gastropods, fish, and oolitic limestones as well as local large-scale wave ripples. Interestingly, Stone (1991) interpreted parts of the Salt Wash Member in northern Colorado as littoral, barrier bar, and lagoonal environments.

Global sea level during the Late Jurassic was somewhat higher than the present level, but not as high as the apparent maximum it reached during the Late Cretaceous. Sea level rose throughout the Oxfordian and Kimmeridgian, then dropped slightly and rose throughout the Tithonian and into the Early Cretaceous (Haq et al., 1987). Regional sea levels in western North America appear to have dropped overall during the Late Jurassic as indicated by the withdrawal of the Sundance sea in the Oxfordian.

The varying paleoenvironmental conditions represented within the Morrison Formation have influenced interpretations of the climate as well. The lithological evidence from much of the formation seems to indicate semi-arid and at least seasonal climates (Bakker, 1986; Peterson and Turner-Peterson, 1987; Turner and Fishman, 1991), but some evidence from plant fossils seems to point to a moderately humid climate, even in more southern areas (Miller, 1987; Tidwell, 1990). Hallam (1994) noted that globally the Jurassic was slightly warmer and latitudinally more equable than the present day, with seasonal rainfall and possibly some polar ice. Douglass and Johnson (1984) noted that the Morrison climate was likely "moderate" and that the latitude of the area that is now central Wyoming was around a rather high-sounding 58 degrees north during the Late Jurassic.

Computer simulations of average Kimmeridgian surface temperatures suggest that western North America, in the area of Morrison deposition, was 4–20 degrees C in the northern winter and 24-36 degrees C in the summer in one model, and 0–16 degrees C in the winter and 20–36 degrees C in the summer in another (Valdes, 1994). The differences between the two models resulted from different sea surface temperature assignments. Interestingly, the differences in temperature between the models were more extreme in the northern hemisphere in general. Average precipitation estimates for the Morrison outcrop region were semi-arid at approximately 1–2 mm/day for the winter months and <1mm/day for the summer months (Valdes, 1994). The calculations of Retallack (1997) gave an average precipitation of about 1.6–2.5 mm/day.

Paleontology Overview

The Morrison Formation yields a rich vertebrate fauna including fish, frogs, salamanders, crocodiles, turtles, pterosaurs, lizards, mammals, and more than twenty genera of dinosaurs (Figs. 4 and 5), including the well-known forms *Allosaurus*, *Stegosaurus*, and *Apatosaurus* (Simpson, 1926a; Ostrom and McIntosh, 1966; Dodson et al., 1980; Britt, 1991). More than 200 sites producing these vertebrates have been found in Colorado, Wyoming, Utah, Montana, South Dakota, New Mexico, and Oklahoma.

Invertebrate fossils known from the Morrison Formation include a crayfish from the Mygatt-Moore Quarry and gastropods, conchostracans, ostracods, and bivalves from numerous localities (Chure et al., 1998). The gastropods include freshwater

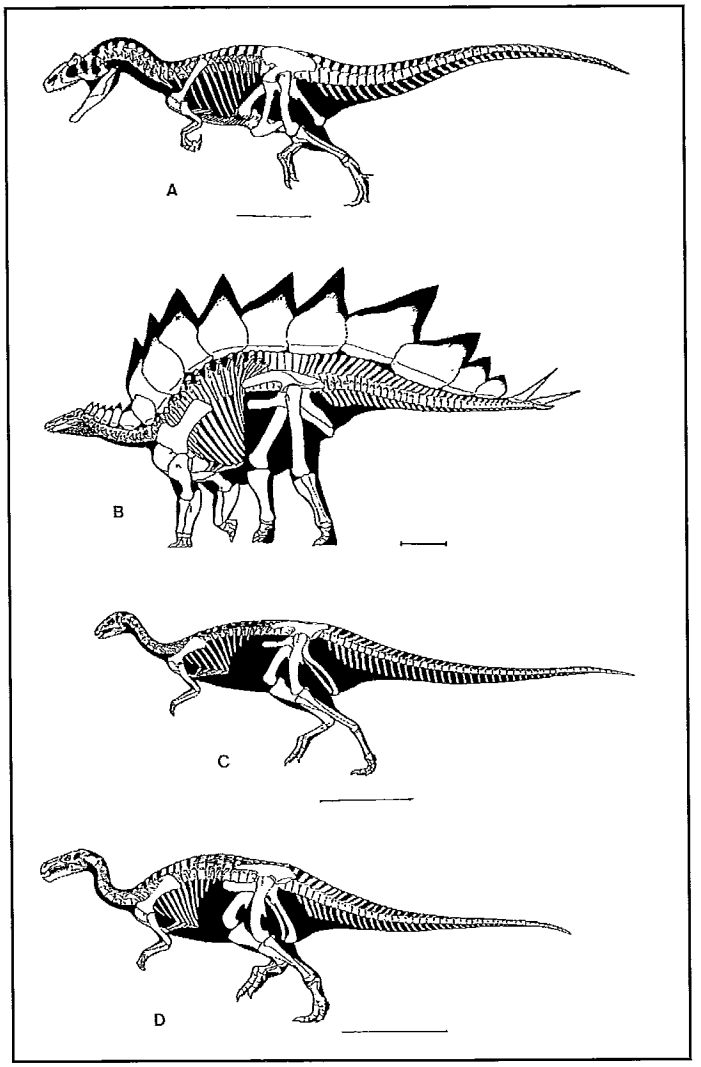

FIGURE 4. Skeletal reconstructions of several common Morrison Formation dinosaurs. **A**, *Allosaurus*; **B**, *Stegosaurus*; **C**, *Dryosaurus*; **D**, *Camptosaurus*. Scale bars = 1 m (A, D); 50 cm (B, C). Reconstructions by Greg Paul.

and, possibly, terrestrial forms (Evanoff et al., 1998).

The first vertebrate tracks in the Morrison Formation were reported by Marsh (1899) from the southern Black Hills in western South Dakota. In the 1930s Bird (1939a,b) and MacClary (1936, 1938) reported on what is still the largest tracksite in the Morrison Formation, a locality along the Purgatoire River in southeastern Colorado that was later restudied in detail (Lockley et al., 1986; Prince and Lockley, 1989). Since this time the number of tracksites has grown to nearly 50, with tracks of sauropod, theropod, and ornithopod dinosaurs and crocodilians, pterosaurs, and possibly turtles represented at various sites (Lockley et al., 1998).

Trace fossils of invertebrates are present as well (Hasiotis and Demko, 1996a,b), and these indicate the presence of ants, beetles, termites, snails, and crayfish. The traces are particularly common in sandstone units in the formation throughout the outcrop area.

Though it is better known for its remains of dinosaurs and other vertebrates, the Morrison Formation has produced one of the most diverse Mesozoic floras in the world. Plant fossils are present at a number of sites (e.g., Brown, 1972, 1975), and some plant remains are mixed in with vertebrate quarry material (e.g., Tidwell et al., 1998). The plants from the Morrison Formation in-

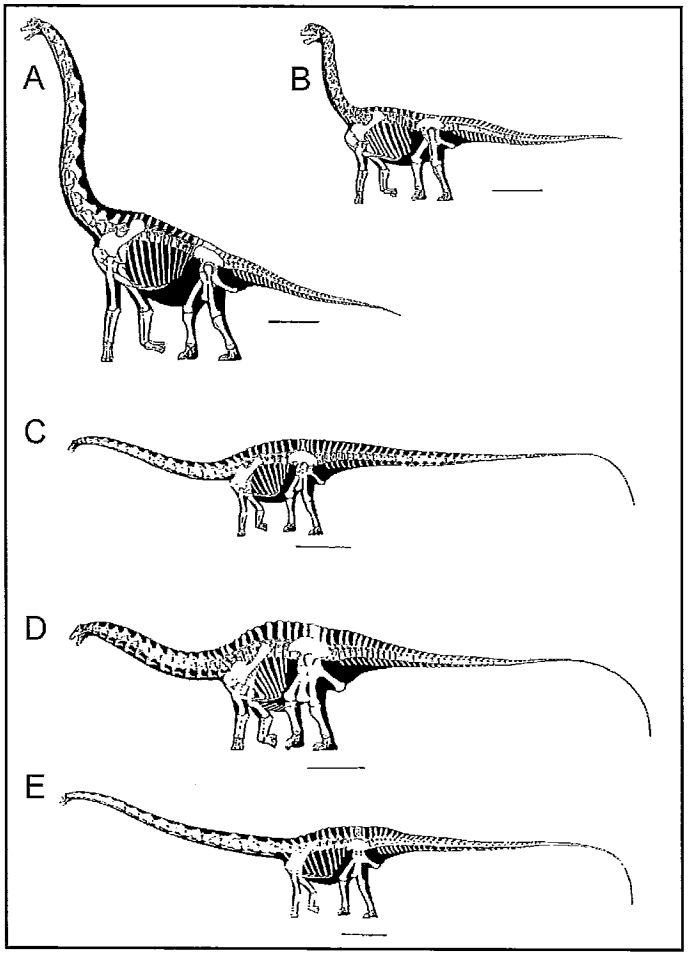

FIGURE 5. Skeletal reconstructions of some Morrison Formation sauropod dinosaurs. **A**, *Brachiosaurus*; **B**, *Camarasaurus*; **C**, *Diplodocus*; **D**, *Apatosaurus*; **E**, *Barosaurus*. All scale bars = 2 m. Reconstructions by Greg Paul.

clude genera of algae, bryophytes, ferns, horsetails, seed ferns, cycadophytes, ginkgos, and conifers. The 35 known genera include 77 species of megafloral remains (Carpenter, unpublished). Pollen and other plant microfossils occur at a number of different localities throughout the Rocky Mountain region and have been assigned to 104 microfloral species. Between micro- and megafloral preservation types, plants are not as rare in the Morrison Formation as it might seem (Chure, 1992). Silicified wood is relatively common (Tidwell and Medlyn, 1993), but compression plant macrofossils occur at only a few sites, and most of these are in one area of Montana north of the northernmost occurrence of good vertebrate material in the formation. Some plant macrofossil compressions have also been found in southeastern Utah. Conifers and cycadophytes are the most common, wide-ranging, and diverse elements of the flora.

Based on plants, the Morrison Formation environment appears to have been seasonally wet with no evidence of freezing. Conifers were probably scattered, with a lower story of cycadophytes and tree ferns, and an understory of ferns (Miller, 1987). Ginkgos were scattered among the conifers. In the absence of grass or any type of angiosperm, pteridophytes may have formed the main ground cover during the Jurassic, even in areas away from other vegetation, although Tiffney (1997) pointed out that the dependency of these types of plants on water for the reproductive cycle would have limited their local range, particularly in semi-arid to arid climates. Thus, some areas of the Morrison floodplain may have lacked vegetation.

Global Late Jurassic Deposits

The vertebrate faunas from several other formations around the world demonstrate varying degrees of similarity to the fauna of the Morrison Formation. These deposits include the Late Jurassic-Early Cretaceous Purbeck Formation and Late Jurassic Kimmeridge Clay of England, the Late Jurassic Guimarota Coal Mine deposits of Portugal, the Late Jurassic Tendaguru Beds in Tanzania, the Middle-Late Jurassic Shangshaximiao Formation in China, and the Late Jurassic Solnhofen Plattenkalk in Germany.

The Purbeck Formation shares several microvertebrate genera in common with the Morrison Formation, including the sphenodontian *Opisthias*, the scincomorph lizard *Paramacellodus*, and the anguimorph lizards *Dorsetisaurus* and *Parviraptor* (Hoffstetter, 1967; Evans, 1994, 1996). In addition to these, the mammalian microvertebrate faunas in the Purbeck and Morrison share the genera *Ctenacodon* and *Amblotherium* and contain similar members of the Triconodonta as well, though these are not of the same genera (Simpson, 1928). The Early Cretaceous age part of the Purbeck has been found recently to contain the Morrison symmetrodont mammal genus *Tinodon* (Ensom and Sigogneau-Russell, 2000). Few good dinosaur specimens are known from the Jurassic section of the Purbeck but a close relative of one, *Echinodon*, is now known from the Morrison Formation as well (Galton, 2002).

The Kimmeridge Clay has produced remains of brachiosaurids, including *Bothriospondylus*, a stegosaur (*Dacentrurus*), theropods, and the ornithopod genus *Camptosaurus*, which also occurs in the Morrison (Weishampel, 1990).

The Guimarota Coal Mine in Portugal contains several genera that also occur in the Morrison Formation, including the choristodere *Cteniogenys*, the scincomorph lizard *Saurillodon*, and the anguimorph lizards *Dorsetisaurus* and *Parviraptor* (Evans, 1996). The Guimarota deposits also produced *Haldanodon*, a docodontid similar to the Morrison genus *Docodon* (Lillegraven and Krusat, 1991), and a number of other mammalian genera (see chapters in Martin and Krebs, 2000). Unnamed units in Portugal have also produced dinosaur species assigned to the Morrison genera *Camarasaurus* and *Brachiosaurus*, and have also produced the stegosaur *Dacentrurus* (Weishampel, 1990). The Lourinhã Formation in Portugal has yielded *Allosaurus fragilis*, a species of dinosaur also known from the Morrison Formation (Pérez-Moreno et al., 1999). The theropod genera *Torvosaurus* and *Ceratosaurus* have also been reported from the Late Jurassic in Portugal (Mateus and Antunes, 2000a,b).

The Kimmeridgian-Tithonian age Tendaguru Beds in Tanzania were worked mainly by E. Fraas, W. Branca, and W. Janensch from 1907 to 1912 (Sues, 1997) and produced the dinosaur fauna most similar to the Morrison, including genera that occur in both areas. Among these are *Brachiosaurus*, *Dryosaurus*, *Elaphrosaurus*, ?*Allosaurus*, and *Barosaurus* (Weishampel, 1990). The Tendaguru deposits also produced a stegosaur, *Kentrosaurus*, which is fairly different from the Morrison genus *Stegosaurus*. The deposit represents a nearshore terrestrial paleoenvironment, and the freshwater units are interbedded with marine layers (Russell et al., 1980).

Raath and McIntosh (1987) identified the sauropod genera *Brachiosaurus*, *Barosaurus*, and ?*Camarasaurus* in the Upper Jurassic Kadzi Formation of northern Zimbabwe. All three of these are known from the Morrison Formation as well; Raath and McIntosh (1987) also identified the Tendaguru sauropods *Dicraeosaurus* and *Tornieria* in the Kadzi material.

The Oxfordian age Shangshaximiao Formation in China contains a purported allosaurid (*Szechuanosaurus*), several species of one genus of "cetiosaurid" sauropod (*Omeisaurus*), another

very long-necked sauropod (*Mamenchisaurus*), and two stegosaurs (*Tuojiangosaurus* and *Chungkingosaurus*) (Weishampel, 1990). The sauropods from this formation are particularly different morphologically from those of the Morrison, with several of the forms having unusually elongate necks (McIntosh et al., 1997). The stegosaurs from the Shangshaximiao have relatively primitive characteristics compared with *Stegosaurus* but are otherwise roughly similar to stegosaurs from other areas (Galton, 1990, 1997).

The Solnhofen Plattenkalk in Germany is mid-Tithonian in age and contains a diverse fauna of vertebrates , including sharks and rays, bony fish, turtles, ichthyosaurs, a plesiosaur, lizards, sphenodontians, crocodilians, pterosaurs, the theropod *Compsognathus*, and the bird *Archaeopteryx* (Barthel et al., 1990). The paleoenvironment is that of shallow marine lagoons in an area with numerous islands.

METHODS

The primary goal of this study was to identify possible temporal, geographic, or paleoenvironmental variations in the distributions of vertebrate taxa and guilds in the Morrison Formation. Although guilds were originally defined as groups of related animals that make their living the same way, it has more recently come to mean simply a group of species with a similar ecological function (Rosenzweig, 1995). Changes in paleoecological structure within the formation were identified using the varying numbers of taxa, relative abundances, and biomass of genera in concert with taxon-free characterization of the animals (Damuth et al., 1992; Wing et al. 1992). This method allows groupings of different, sometimes unrelated, genera into guilds united by their similar paleoecological roles and facilitates analysis of the ecological structure of a paleocommunity. The ecological characterization of each known taxon from the Morrison Formation included the estimated body mass, the feeding mode, and locomotion/habitat mode. Two other applicable variables listed by Damuth et al. (1992), feeding habitat and shelter habitat, are not included, as in almost all cases in which these could be reliably determined, they were the same as the taxon's locomotion/habitat mode. With the characterizations combined with the census data, the changes can then be identified in diversity, relative abundance, and biomass of different guilds through time, across geographic areas, and in different environments.

Database Compilation

The main database in this study consisted of faunal lists and specimen counts from as many known Morrison Formation localities as possible. Compiling this database involved three main steps: 1) listing the known localites, 2) listing the known taxa from each site, and 3) counting specimens of each taxon from each site. The list of localities was compiled in the early years of the study and was drawn from published references on the Morrison Formation in general and on specific sites, from personal knowledge of smaller sites, from personal communications with other workers, and from records and catalogs in natural history museums. Faunal lists were compiled from the same sources for respective sites. Specimen counts were compiled from study of museum collections, references, personal communication, and quarry visits, particularly for smaller sites. Larger localities were counted from museum catalogs, collections, and records, and in some cases (such as the Carnegie Museum, McIntosh, 1981) from published references.

Work in museums included censusing and study of collections (and catalogs), noting taphonomic characteristics of bones, and noting quarry matrix in some cases. In cases in which computerized catalog printouts were available, collections were surveyed to note possible associations of specimens. Museums and collections that were visited in order to compile the specimen counts include: University of Colorado Museum (Boulder), Denver Museum of Nature and Science (Denver), Dinosaur Depot (Cañon City), Museum of Western Colorado (Grand Junction), BYU Earth Science Museum (Provo), College of Eastern Utah (Price), New Mexico Museum of Natural History (Albuquerque), Dinosaur National Monument (Jensen), Wyoming Dinosaur Center (Thermopolis), Sheridan College (Sheridan), Tate Museum (Casper), University of Wyoming (Laramie), South Dakota School of Mines & Technology (Rapid City), Science Museum of Minnesota (St. Paul), Field Museum of Natural History (Chicago), Cleveland Museum of Natural History (Cleveland), Museum of Comparative Zoology (Cambridge), Yale Peabody Museum (New Haven), American Museum of Natural History (New York), National Museum of Natural History (Washington), Oklahoma Museum of Natural History (Norman), Carnegie Museum of Natural History (Pittsburgh), Utah Museum of Natural History (Salt Lake City), and Los Angeles County Museum of Natural History (Los Angeles).

Counting Method

One of the main considerations in the counting of specimens was which method to use. Because the Morrison Formation contains both articulated skeletons and isolated bones, it is necessary to decide how to count each of these. Badgley (1986) reviewed some of the common methods for counting relative numbers of individuals for mammalian assemblages; these include minimum number of individuals (MNI), number of identified specimens (NIS), and minimum number of elements (MNE). The MNI method is best suited to deposits in which there has been limited transport and in which the probability of association of elements is medium to high. The NIS method, on the other hand, works best for sites that show evidence of current transport of bones prior to burial and where the probability of association of elements is low. Both methods were used for different sites in the Morrison. In general, MNI counts were used for larger animals such as dinosaurs when they were disarticulated, and NIS counts were used most often for small, non-dinosaurian vertebrates which were also disarticulated. The main questions asked when deciding which method to employ for a locality were: 1) what is the likelihood that any two bones of one taxon from the site belong to the same individual and 2) does this likelihood vary among species in the sample (J. Damuth, pers. comm., 1997)? MNI counts were employed when the answers to those questions were believed to be "high" and "yes," respectively, and NIS counts were employed in a "low" and "no" situation. In some situations both methods were employed at one locality, but this was generally done for consistency, as larger dinosaurs were almost always counted with the MNI method. In practice, microvertebrate sites (at which NIS counts worked best for the small taxa) contained a few larger dinosaurian specimens, which were counted by MNI methods, but the MNI counts were essentially the same as NIS counts, as there was rarely evidence for more than one or two individuals of any dinosaurian taxon in these cases.

For MNI counts at larger sites, catalog numbers of specimens, their identifications, and the preserved elements were entered into a spreadsheet and later sorted by taxon and element for each quarry. The MNI count for one taxon then was derived from the most common identifiable element.

Counts were difficult at localities where crocodilian taxa were represented mainly by teeth. Even though NIS counts worked on most other taxa at the sites, this method created problems with crocodilians (and potentially other reptiles) due to continuous shedding of teeth. MNI counts at these sites would force us to assume that many teeth had come from just one individual,

which is unlikely (in fact, it is possible that no two crocodilian teeth from a site came from one animal). On the other hand, NIS counts of crocodilian teeth would overestimate the number of animals. This problem was addressed by retaining the NIS counts for crocodilian teeth but scaling the counts down based on the estimated average number of teeth crocodilians would have produced. This method attempted to estimate the degree to which crocodilians were more likely to be represented in the fossil record due to continuous production and shedding of teeth. An estimate of crocodilian tooth replacement rates (Erickson, 1996a), combined with estimates of crocodilian growth rates and average life expectancy (McIlhenny, 1935; Dodson, 1975; Kushlan and Mazzotti, 1989), were used to determine the approximate number of teeth produced per socket. Morrison Formation crocodilians probably reached ages of up to 35–50 years, but average life expectancies are estimated to have been about 4.5 years; at this average age, and assuming tooth replacement rates of 3–4 teeth/socket/year, it is estimated that the crocodilians produced an average of 16 teeth/socket. Thus, crocodilians were, if represented mainly by teeth, about 16 times more likely to be represented in the fossil record, so the tooth counts of crocodilians from appropriate quarries were divided by this number to approximate the correct NIS counts. Similar scaling can be done for some dinosaurian groups as well (Erickson, 1996b).

Before counts could be made on specific taxa from different localities, it was necessary to also list the known taxa from the Morrison Formation. This list had to be finalized before any counts could be made, and the finalization process included deciding which taxa were to be considered valid in this study. The systematics of groups from the Morrison Formation used in this study were based on a combination of sources including Gauthier (1986), Carroll (1988), McIntosh (1990a), Upchurch (1995), Galton (1990), Sues and Norman (1990), Norman and Weishampel (1990), and McKenna and Bell (1997). The validities of many taxa are in question and opinions differ on which may be valid, synonymous, or based on insufficient material to judge. The taxa were analyzed at the generic level, as in addition to questions about the validity of some species, the majority of the material that has been collected is not identifiable below the generic level. In a few cases, however, two forms of a genus were recognized as separate taxa. This was done when the distinction was clear morphologically and when it had some effect on the ecological characterization of the taxa. These cases include: 1) *Ceratodus robustus*, which is significantly larger than the other forms of lungfish assigned to various species of *Ceratodus* and is in a different weight category entirely; 2) *"Diplodocus" hayi*, which is probably a new genus, as its postcranial skeleton is less like *Diplodocus* than that genus is to *Barosaurus*; 3) *Camarasaurus supremus*, which is far larger than other species of *Camarasaurus* and seems to occur mainly near the top of the formation; and 4) *Haplocanthosaurus delfsi*, which is in a different weight category from other specimens assigned to *H. priscus* and appears to be distinct from them.

Molnar (1990a) argued that, based on skeletal material alone, it is probably more likely that two biological species will be mistaken for one than one would be for two. This may be true for smaller animals such as mammals, but it is difficult to imagine that the diversity of sauropods, for example, has been underestimated, especially given the historically heavily-split nature of sauropod taxonomy. In any case, the generic level analysis necessary for this study to have sufficient identified material means that the diversity of mammals at least is very likely underestimated, as some mammal genera from the Morrison Formation seem to have two valid species. Unfortunately, however, there would have been significantly less identified material available for analysis if only material identifiable to species level were used. The details of the taxonomic situation for this study are covered in the Systematics section.

Specimen counts from the Cleveland-Lloyd Quarry in Emery County, Utah, included only the taxa other than *Allosaurus*, as there are nearly nine times as many individuals of this theropod as there is any other type of animal in the deposit. The probability of an usual taphonomic process being involved in the preservation of this deposit necessitated including only other animals in the count along with at least one *Allosaurus*. Similarly, at the Howe Quarry, where there are at least a dozen diplodocid sauropods and a number of other, less common animals, only the individuals that have been positively identified so far have been included in the count. Very little of the Howe Quarry material has been prepared, and only these were included in the count; the 12 or so individuals are estimated based on R. T. Bird's quarry map (Bird, 1985).

Quarry Data

Each quarry also had attributes associated with it that were collected for the quarry list. These attributes were important for comparing the distributions of the faunas within each quarry. The three main quarry attributes used were geographic location, stratigraphic level, and lithology (Table 1). These were used to estimate and categorize the quarry's fauna by geographic tier, relative stratigraphic level, and paleoenvironment of preservation. Rough geographic locations of the quarries were not difficult to determine, and in general, this allowed all quarries to be categorized by North-South and East-West geographic tiers. The outcrop area of the Morrison Formation was subdivided into roughly equal thirds from north to south and then from east to west. Because not enough quarries existed in some areas for there to be a specific Northeast zone, for example, the tiers were characterized only by the north-south and east-west zonations.

The stratigraphic levels for the quarries were largely de-

TABLE 1. Attributes and categories used to characterize Morrison Formation quarries for this study.

GEOGRAPHIC TIERS*:	
North	
Middle	
South	
West	
Central	
East	
STRATIGRAPHIC LEVEL:	
Top	Zone 6
	Zone 5
	Zone 4
	Zone 3
	Zone 2
Bottom	Zone 1
LITHOLOGY/ENVIRONMENTS:	
Channel Sands	
Overbank Sands	
Type I Ponds	
Type II Ponds	
Type I Poorly Drained Floodplain	
Type II Poorly Drained Floodplain	
Well Drained Floodplain	
Lacustrine Limestone	

*defined by north-south and east-west thirds along the geographic range of the formation.

pendent on a formation-wide study of the relative stratigraphic positions of major quarries. Until just a few years ago no analysis of the temporal variation within the formation would have been possible because no correlation had been done or even atttempted over the lateral extent of the formation. Recently, however, this has been done, and preliminary data on the relative chronostratigraphic positions of many of the quarries are available (Turner and Peterson, 1999). Trujillo (2002) noted some potential problems with correlation techniques used in the Morrison Formation, so the relative positions of the quarries should be regarded as tentative.

The stratigraphic zones used in this study are based on an early version of Turner and Peterson's Dinosaur Zones. These were determined by plotting the positions of more than 100 Morrison Formation quarries and the ranges of different dinosaur taxa; zone boundaries were drawn at levels at which noticable increases or decreases in dinosaur diversity were apparent. Thus, the thicknesses of the zones differ. The zones were numbered 1 through 4, upward through the section, by Turner and Peterson (1999). They initially, before publication, subdivided their Zone 3, into a lower Zone 3A and an overlying 3B, and I subdivided Zone 3B into upper and lower subzones due to the high number of quarries in the subzone. My analysis was done using Turner and Peterson's (1999) unpublished zones; thus, I used a system with six vertebrate Zones (1–6 from bottom to top), which relates to the Turner and Peterson (1999) zones as in Figure 6.

The quarry lithologies were used to determine, as close as possible, the depositional paleoenvironments. The paleoenvironmental classifications (Table 2) were based largely on the environments and lithofacies of Dodson et al. (1980), but as the study

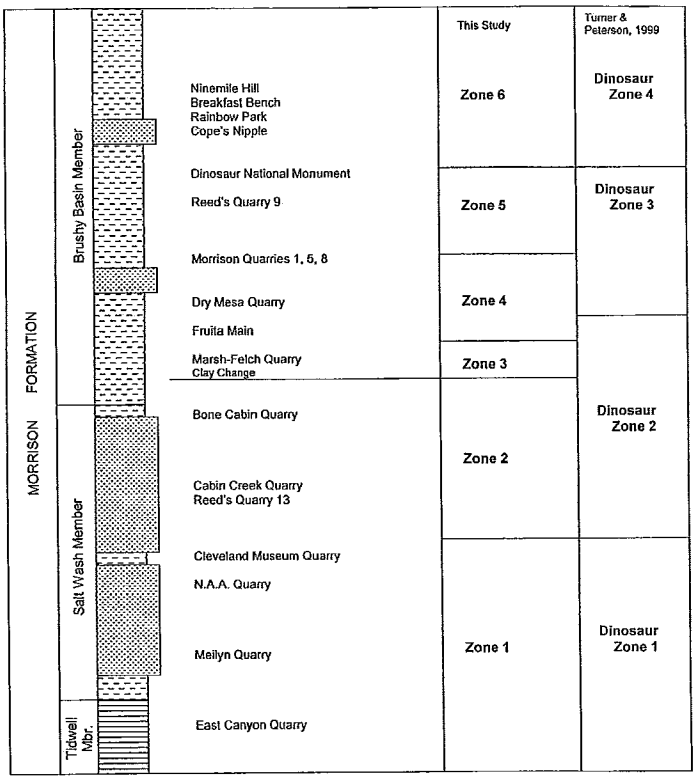

FIGURE 6. Stratigraphic zones used in this study in relation to a generalized section of the Morrison Formation and to approximate relative postions of several major quarries. Also shown for comparison are dinosaur zones of Turner and Peterson (1999). Zones used here were based on an earlier version of Turner and Peterson's work. Generalized section based on Dinosaur National Monument.

went on, it was determined that some more detailed categories could be defined. For example, Lithofacies A of Dodson et al. (1980) was subdivided into channel and overbank sand units, and the equivalent of Lithofacies C was subdivided into several categories based on lithologies that were less well known at the time of that study and on taphonomic characteristics of the microvertebrates at some localities. Type 1 Ponds include sites such as Quarry 9, at which siltstones and fine sandstones predominate and contain abundant disarticulated remains of microvertebrates; this type of deposit is essentially the same as the Type I taphofacies of Foster (2001). Type 2 Ponds include the Fruita Paleontological Area overbank sites with slightly finer-grained deposits and volumetrically more rare, but more often articulated microvertebrate remains; this type of deposit is the same as the Type II taphofacies of Foster (2001). Type 1 Poorly Drained Floodplain deposits are similar to the original Lithofacies C definition of Dodson et al. (1980). Type 2 Poorly Drained Floodplains consist of dark gray and black mudstones and occur mainly near the top of the formation. This lithology is found at Morrison Quarry 10 and several other areas, often near the top of the formation (Turner and Peterson, 1999), although at some sites it is unclear whether or not the lithology is part of the lower beds of the overlying Cretaceous formations. These dark mudstone units probably represent swampy floodplain deposits. The Lacustrine and Well-Drained Floodplain paleoenvironments were retained from Lithofacies D and B of Dodson et al. (1980). Well-Drained Floodplain deposits include paleosols Retallack (1997) described as representing open forest areas.

Collection of the quarry data came from published references on well-studied sites, from museum records and matrix samples, from Fred Peterson's field notes (United States Geological Survey, Denver), and as much as possible, from personal visits to the quarries. Work during field visits to sites included measurement of stratigraphic levels of some quarries and study of quarry sedimentology and taphonomy.

Ecological Categories

Ecological characterizations of the taxa defined for this study were based on various sources; ecological variables and categories are listed in Table 3. Mass estimates were based on comparisons with modern, related forms when such were available (fish, frogs, salamanders, sphenodontians, crocodilians), on measurements obtained during this study using the formulae of Anderson et al. (1985), and on references with mass estimates of Morrison taxa or related forms. Some of the references include: Wellnhofer (1991) for pterosaurs; Dodson et al. (1980) for various dinosaur and non-dinosaur taxa; Paul (1988a) for theropods; and Bakker (1980) for mammals. Most mass estimates for sauropods, ornithopods, and stegosaurs were based on personal measurements. The technique of Anderson et al. (1985) uses circumference measurements of the humerus and femur in quadrupedal animals and femur in bipedal animals to estimate the mass. The equations

$$\text{Log}_{10}W = 2.73(\text{Log}_{10}(\text{Ch} + \text{Cf})) - 1.11(\text{quadrupedal})$$

and

$$\text{Log}_{10}W = 2.73(\text{Log}_{10}\text{Cf}) - .76(\text{bipedal})$$

give approximate mass estimates for the dinosaurs, where W is the mass in grams and Ch and Cf are the humerus and femur circumferences, respectively, in millimeters.

Bakker's (1980) estimate of 10–100 g for the weight of most of the Early Jurassic mammals was one of only two published that I found, although he does not state the method used for the estimation. Bakker's (1980) estimate was used for most of the Late

TABLE 2. Characteristics of the Morrison Formation paleoenvironmental categories used in this study.

Abbreviation	Type	Environments	Lithologies	Lithofacies of Dodson et al. (1980)	Taphonomic Characteristics	Representative Quarries
CH	Channel	Fluvial channels	Sandstone, fine to gravelly; some cross-beds	A	Disarticulated to articulated dinosaur remains in lag deposits; rare microvertebrates	Dinosaur National Monument Main; Dry Mesa; Bone Cabin
OS	Overbank Sands	Near-channel sand splays	Sandstone, med.-fine grained; siltstone; thin	A	Disarticulated to articulated dinosaur remains; rare microvertebrates	Cleveland Quarry Garden Park
PD1	Type 1 Pond	Near-channel ponds and fine splays; abandoned channel fill ponds	Siltstone, claystone, fine sand, clay clasts	C, A	Disarticulated to articulated dinosaur remains; relatively abundant disarticulated microvertebrate remains in thin but dense accumulations closely associated vertically with sandstones; Taphofacies I of Foster (2001)	Quarry 9 (Como); Small Quarry; Little Houston Quarry
PD2	Type 2 Pond	Near-channel ponds and fine-grained splays	Claystone, siltstone, very fine sand	C	Disarticulated to articulated dinosaur remains; moderately rare to common disarticulated to articulated microvertebrate remains in low-density accumulations with less distinct layering than Type 1; sometimes laterally associated with sands; Taphofacies II of Foster (2001)	Quarry 4 and Tom's Place (Fruita Paleo Area); Wolf Creek Quarry
FPP1	Poorly Drained Floodplain - Type 1	Wet areas of floodplain; ponds; near channel or out on plain	Claystone, rare silt; drab and relatively pale colored	C	Disarticulated to articulated dinosaur remains; microvertebrates rare or absent	Reed's Quarry 10; Stovall's Quarry 1
FPP2	Poorly Drained Floodplain - Type 2	Wet areas of floodplain; ponds and swamps; near channel or out on plain	Claystone, rare silt; gray, dark gray, and black; sometimes carbonaceous	C	Disarticulated to articulated dinosaur remains; some mostly disarticulated microvertebrates	Breakfast Bench; Morrison Quarry 10
FPW	Well Drained Floodplain	Higher parts of floodplains and areas with lower water table	Claystone; rare silt; red, maroon, gray	B	Disarticulated to articulated dinosaur remains; microvertebrates absent or rare	Cope's Nipple
LK	Lacustrine	Lakes and large ponds	Limestone; drab claystone	D	Rare dinosaurian remains; microvertebrates rare to absent; tracks relatively common	Purgatoire River; Egg Gulch (croc)

Jurassic taxa, as the mammals of the Morrison Formation are little larger than those of the Early Jurassic, and it is unlikely that any of the mammals weighed more than a kilogram. The triconodont weight estimates were increased slightly over the others, as these mammals are a bit larger than most others in the Morrison Formation. Cifelli and Madsen (1998) calculated masses for Cretaceous triconodonts as large and larger than Morrison triconodonts and obtained estimates less than 1 kg for all.

Because no femora exist for many of the Morrison Formation theropods, the method of Anderson et al. (1985) for mass estimation would not work; Paul (1988a) modeled theropod taxa and estimated the masses, and his estimates were used for consistency among the theropods. Estimates of Dodson et al. (1980) were used for crocodilians and turtles, and Wellnhofer's (1991)

TABLE 3. Attributes and categories used to characterize Morrison Formation vertebrate taxa for this study.

Locomotion/Habitat:	Aquatic
	Semiaquatic
	Terrestrial
	Specialized Terrestrial
	Aerial
Feeding Mode:	Invertivore
	Invertivore/Carnivore
	Omnivore
	Small Carnivore (<50 kg)
	Medium Carnivore (50-400 kg)
	Large Carnivore (>400 kg)
	Low Browser (0-2 m feeding height)
	Medium Browser (1-4 m)
	High Browser (>4 m)
Mass*:	<0
	0-1
	1-2
	2-3
	3-4
	>4

*Categories in Log_{10}(kg)

mass estimates of Morrison pterosaurs were used. In cases of pterosaurs not listed in Wellnhofer's book, the masses were estimated by scaling up the estimated weights of related forms. Most mass estimates of fish, lungfish, frogs, salamanders, and lizards were based on comparison with modern forms.

Each taxon also was assigned to an appropriate weight category based on its mass estimate. These categories were <1 kg, 1–10 kg, 10–100 kg, 100–1000 kg, 1000–10,000 kg, and >10,000 kg. In most figures, these categories are marked at the Log_{10} of the mass.

Locomotion/Habitat categorization was determined based on comparisons with modern, related taxa or on morphological characteristics. The habitat categories were: Aquatic for fully water-bound forms (fish); Semiaquatic for animals that spend various amounts of time in water and on land or are dependent on water (turtles, crocodilians, frogs); Terrestrial for animals that spend most of their time on the land surface (dinosaurs); Specialized Terrestrial for mostly small animals which may be fossorial, scansorial, or arboreal but which, because their postcranial elements are rarely preserved, cannot be futher categorized (mammals, lizards); and Aerial for animals capable of flight (pterosaurs).

Feeding Mode categories included: Invertivores; Invertivore/Carnivores; Omnivores; Small, Medium, and Large Carnivores; and Low, Medium, and High Browsers. Invertivores were mainly small forms considered to have fed largely on adult insects, grubs, worms, and other small invertebrates. Animals were assigned to the group based on: comparison with modern related groups, such as frogs and lizards; on relatively high-cusped, small-crown area, shearing-type molars in mammals; and/or the small size of the animals (implying a dependence on relatively high-protein diet).

Invertivore/carnivores probably fed on invertebrates and some small vertebrates. The types of prey animals used probably differed from one form to another. For example, some aquatic forms may have fed on bivalves, gastropods, and small fish, whereas a terrestrial Invertivore/Carnivore may have fed on insects and small vertebrates.

Omnivores include forms that appear to have fed consistently on two trophic levels, usually plants and small vertebrates or invertebrates. Determination of this group was based on comparison with modern taxa (turtles) or on flat, grinding or relatively blunt-cusped molars in mammals, suggesting animals that fed on seeds or other plant material but which were small enough to have likely fed on insects as well (multituberculates, see Clemens and Kielan-Jaworowska, 1979; docodonts).

Carnivorous taxa are those that fed mainly on other vertebrates (at least as adults). Most of these taxa have sharp, sometimes serrated teeth, but in fossil forms for which no skull is known, the relationship of the animal to other carnivorous forms was assumed to imply a similar life habit. Carnivores included theropod dinosaurs, crocodilians, and pterosaurs, and were subdivided in small, medium, and large categories based on mass estimates. For the purposes of this study, Small Carnivores were those under 50 kg, Medium Carnivores were those between 50 kg and 400 kg, and Large Carnivores were those above 400 kg. Initially, it was hoped that the theropods could be subdivided into guilds based on morphological characteristics in a manner similar to Van Valkenburgh's (1988) work on fossil mammalian predators, but too many of the Morrison theropods are missing key skeletal parts (skulls and forelimbs). The mass subdivision was considered the best method for ecologically subdividing the theropods. Small carnivores, including small theropods and terrestrial crocodilians such as "*Fruitachampsa*," may well have competed with each other for small vertebrate prey items, and probably experienced little competition with large, adult carnivores.

The Herbivorous species were subdivided into Low, Medium, and High Browsers. Low Browsers fed mainly at levels within 2 m of the ground surface, Medium Browsers fed mainly at levels below 4 m, and High Browsers fed mainly above 4 m. Categorization of these animals was based mainly on tooth type and browse level determined by skeletal form. Dinosaurs such as sauropods, ankylosaurs, stegosaurs, and ornithopods have peg-, spoon-, leaf-, or chisel-shaped teeth that are generally agreed to indicate a diet of plants, though it is difficult to determine what type of plants dinosaurs may have fed on the most. The sphenodontid *Eilenodon* is the only non-dinosaurian herbivore (Rasmussen and Callison, 1981a), though this form may well have fed on invertebrates as well. The estimated browsing heights of the dinosaurs were based on normal head heights of the animals as indicated by relatively complete mounted skeletons. Ankylosaurs, stegosaurs, and ornithopods all were considered Low Browsers because their head heights were generally around 1 m. The ornithopod *Camptosaurus* could have gotten a bit higher than 2 m but probably stayed close to the ground. The sauropods were in the Medium and High Browser categories. Medium Browsing sauropods probably overlapped with the Low Browsers to some degree but were able to feed consistently up to 4 m or so. High Browsers include large diplodocids, camarasaurids, and brachiosaurids that were probably feeding significantly higher than 4 m most of the time. The tripodal, high-feeding stance proposed for stegosaurs and diplodocids (Bakker, 1978) is here considered to have been a possible but not habitual feeding mode for these animals.

Data Analysis

Once the data were collected, they were entered into a computer spreadsheet program; taxa were characterized in columns by weight, weight category, and Feeding Mode and Locomotion/Habitat categories. Then the numbers of each taxon in respective geographic tiers, stratigraphic levels, and paleoenvironments were

entered in succeeding columns. In this way, the numbers of specimens of any particular ecological category (e.g., feeding mode) in each of the levels, environments, or tiers could be subtotaled.

Data were analysed with all taxa together and with dinosaurs and non-dinosaurs separated. Among non-dinosaurs, terrestrial animals were also separated out and Aquatic and Semiaquatic species excluded.

The following sections, headed by bold-faced headings, describe the main procedures used to analyze the data.

Correction of Samples to Estimated Population Percentages

Subsequent sheets on the Excel workbook calculated the percent of the sample comprised by each taxon and then the corrected percent of the sample. This method followed that of Dale Russell on Morrison Formation dinosaurs in Coe et al. (1987). Because it is believed that smaller-bodied animal skeletons are more susceptible to preburial destruction, the most common form of taphonomic bias in terrestrial ecosystems appears to be in favor of larger-bodied animals. Russell used a regression based on the work of Behrensmeyer et al. (1979) to "correct" the relative percentages of Morrison Formation dinosaur genera back to theoretical original population values. The work of Behrensmeyer et al. (1979) was based on counts of animals in the Amboseli National Park in Kenya and the numbers of skeletons observed in the same basin; smaller species were consistently under-represented in the skeletal assemblage. Russell (Coe et al., 1987; Russell, 1989) used

$$\mathrm{Log}_{10}\,(N/S) = 1.96 - 0.45\mathrm{Log}_{10}W$$

to correct the percentages of Morrison dinosaurs, where W is the mass of the animal in kilograms. The N/S ratio (animals counted to skeletons observed) from this equation is multiplied by the raw data percentages and normalized to 100% to obtain the corrected population percentage for each taxon. This was done with the data in the present study as well. Additionally, the corrected percentages were multiplied by each animal's mass and normalized to 100% to obtain corrected percent biomass estimates.

It should be pointed out that most of the analyses carried out based on the corrected population percentages are comparisons of relative abundances as opposed to absolute abundances. Hayek and Buzas (1997) noted that, between two samples, relative abundance of a taxon can increase at the same time the density (or absolute abundance) decreases.

Tests for Preservation of Community Structure

Damuth (1982) noted that assemblages of fossil and modern mammals demonstrate a slope of –1.05 +/– 0.25, when the Log_{10} of each species' abundance is regressed on Log_{10} body mass, such that the abundances of species decrease with increasing size. Damuth (1987) also found that the similar density/body mass regression for mammalian, reptilian, and aquatic assemblages demonstrated a –0.75 slope. The slope expected for non-mammalian or mixed abundance/mass regressions, then, should be similar to the –1.05 +/–0.25, and the closeness of the assemblage in question to this slope is a test of the preservation of the true community structure in a fossil assemblage (Damuth, 1982). Corrected abundance data for Rancholabrean and Orellan mammalian assemblages from California and South Dakota are close to this slope (Damuth, 1982); the Rancholabrean sample is within the expected range but the Orellan sample from the White River Group is –0.72, just below the lowest expected slope (–0.80), indicating some taphonomic bias in favor of larger bodied animals.

This test was applied to the Morrison Formation data in this study to estimate potential taphonomic bias present in the samples, even after correction. First, however, it was necessary to make some adjustments.

In this comparison, it is necessary to correct some of the relative abundances further to offset energetic and reproductive output differences between suspected homeotherms and poikilotherms (Damuth, pers. comm., 1998). Homeotherm population densities would have been 1/30th those of poikilotherms but would have reproduced 2–3 times more rapidly. For this reason, the homeotherm abundances need to be adjusted upward 10–15 times because only 1/10th to 1/15th the number of dead individuals would have been produced over time by the small mammals compared to poikilotherms of the same size. The Morrison mammals were probably homeothermic, though perhaps not to the same degree as modern mammals, and lizards, turtles, crocodilians, and other reptiles with related modern counterparts, are generally thought to have been poikilothermic. The reptiles, then, were not increased in abundance for this test, but the multiplied increase of the mammal abundances for this study was set at 10 times. However, the nature of dinosaurian metabolic level has been debated, and certainly not resolved, so whether or not to increase these animals' relative abundance levels was difficult to decide.

Bakker (1972, 1980) argued in favor of tachymetabolic, homeothermic dinosaurs in all groups, based on predator/prey ratios, bone histology, and comparisons with distributions of modern large vertebrates. Paul (1994) seemed to agree with the high metabolic rate theory, but some authors (Spotila et al., 1973; Spotila, 1980) feel that dinosaurs were "ectothermic homeotherms" that maintained high body temperatures but did not have high metabolic rates. They pointed out that a number of active animal groups maintain high body temperatures but that they do it by different strategies, including large size, metabolism, and behavior (i.e. sunning). Bakker (1980) argued that if large size were enough to maintain high temperatures, why are there no large modern reptiles in areas where large mammals live and why would large mammals waste energy on high metabolism when it wasn't necessary? Farlow (1980), on the other hand, pointed out dangers in the use of predator/prey ratios to infer theropod metabolic rates. Farlow noted, in particular, that, with no real idea of how predators concentrated their feeding on various prey, it is difficult to be certain the ratios are real, as a predator that feeds on 10 different prey species but focuses mainly on one will actually demonstrate a higher ratio than if it fed more evenly among the prey species. Other authors have argued that, in some groups at least, endothermy was impossible (Weaver, 1983) and/or unnecessary (Colbert, 1993). Ruben et al. (1997) noted lack of respiratory turbinates in dinosaur specimens they studied as arguing against endothermic dinosaurs. A large number of studies, however, have concluded that while high metabolic rates in dinosaurs are possible, the evidence is not conclusive and more likely the various dinosaur groups demonstrated a range of "intermediate" metabolic rates between the familiar, modern bird/mammal and reptile end-members (de Riqlès, 1980; Ostrom, 1980a; Farlow, 1990; Farlow et al., 1995; Reid, 1997). Hopson (1980) studied the relative brain size of dinosaurs as an indicator of metabolism and concluded that the relative intermediate levels include: sauropods as nearly reptilian to reptilian, ankylosaurs and stegosaurs as slightly higher, ornithopods and theropods as higher than that, and the small "coelurosaur" theropods as very high and nearly bird-like in metabolism.

This last series of metabolic levels was used for the Morrison Formation dinosaurs to correct for the abundance comparisons. The test for preservation of community structure was done without correction to intermediate levels for dinosaurs, with intermediate levels, and with endothermic levels to compare the results.

For the intermediate metabolic levels the dinosaurs were corrected by factors of 3 for ankylosaurs and stegosaurs, 5 for most theropods and ornithopods, and 7 for the small ("coelurosaur") theropods. The sauropods were considered poikilothermic and thus were not increased. The mammals were increased by the factor of 10 as previously mentioned.

Group Occurrence and Sample Size

The number of localities at which groups of taxa are present was graphed versus the Log_{10} total number of specimens at the localities. This was done to see what groups were most common at lower sample sizes and to see what sample size was necessary to preserve most groups known from the formation.

Diversity by Sample Size

The number of specimens at each quarry was graphed versus the number of taxa from each quarry for each stratigraphic level and paleoenvironment. This was done to see if there was any connection, regardless of sample size, between the stratigraphic level or paleoenvironment and diversity.

Sample Comparison By Rarefaction

Diversities within each stratigraphic level were compared using the rarefaction method of Tipper (1979), which was based on equations of Hurlbert (1971) and Heck et al. (1975), for the total number of specimens and taxa within each stratigraphic level. The Sanders (1968) method gives a reasonable estimate of diversity at lower sample sizes but is not as accurate as some computer-run methods and tends to overestimate the diversities (Gotelli and Graves, 1996; Hayek and Buzas, 1997). To give the basic idea of the rarefaction process, however, the Sanders calculation of the expected number of taxa at a given lower sample size can be expressed as

$$X = ((100 - C) / ((1/N) \times 100)) + S$$

where X is the expected number of taxa; N is the selected number of specimens in the new, smaller sample; S is the number of taxa with abundances greater than or equal to 1/N; and C is the cumulative percent of the sample represented by taxa with abundances greater than or equal to 1/N. The more accurate technique of Tipper (1979), which is based on more complex equations, was used in this study.

The rarefaction process involves the assumptions that: 1) sampling has been sufficient to accurately represent each collection; 2) the collections are taxonomically similar and at least drawn from similar communities; and 3) sampling techniques were fairly similar for each collection (Gotelli and Graves, 1996). Of these assumptions, 2 and 3 are, perhaps, the least problematic for the Morrison Formation sample, but I am skeptical that collecting from the lower stratigraphic levels has been sufficient.

Diversity Test—Simpson Index

Diversity by stratigraphic level was tested by calculating the Simpson Index for each level (Simpson, 1949). The Simpson Index is:

$$SI = \Sigma((n^2-n) / (N^2-N))$$

where n is the number of individuals of a species and N is the number of specimens in the whole sample. The upper limit of SI is 1, when the sample consists entirely of specimens of one species. The lower limit is 0 when each specimen represents a different species; thus the higher the SI, the lower the diversity.

Chi-Square Test for Homogeneity

In order to determine if any observed differences in the diversities and relative abundances of ecological guilds between stratigraphic levels, geographic regions, or paleoenvironments were real or possibly the result of differences in sample size, chi-square tests of homogeneity were conducted for the data in a graph to the 0.05 significance level. For this test the test statistic value used was:

$$X^2 = \Sigma\text{all cells } (O - E)^2 / E$$

where O is the observed number of specimens in a cell of the data spreadsheet and E is the estimated expected value calculated for that cell based on

(row total)(column total) / total of row or column

because totals of all rows and all columns will add to the same amount. X^2 values exceeding the 0.05 significance critical value for the given degrees of freedom were taken as indicating likely significant variation in paleoecological structure for the given test. Unfortunately, not all expected values were high enough to allow the test to be run on all the cells in a contingency table (expected values must be > 5); for many of the graphs the chi-square test could only be done on the cells with the highest values, and significance was determined from these.

Graphs of Data

The Locomotion/Habitat categories, Feeding Mode guilds, and weight categories were graphed by stratigraphic level and, in some cases, by geographic tier and paleoenvironment. Measurements of the guilds and weight categories were by number of taxa, corrected number of individuals, and corrected biomass.

Predator/Prey Ratios

Predator/Prey ratios were determined using the same data described above. Corrected biomass percentages of carnivorous taxa were added and compared as a percentage of the total biomass. Carnivorous taxa were included in the total biomass because larger carnivores could have fed on smaller ones as well as on smaller individuals of their own taxon (Bakker, 1980).

Abbreviations

Abbreviations of museums used in this report include: AC – Amherst College; AMNH – American Museum of Natural History; BYU – Earth Science Museum, Brigham Young Unversity; CEUM – Prehistoric Museum, College of Eastern Utah; CM – Carnegie Museum of Natural History; CMNH – Cleveland Museum of Natural History; DMNH – Denver Museum of Nature and Science; DNM – Dinosaur National Monument; FMNH – Field Museum of Natural History; LACM – Los Angeles County Museum of Natural History; MCZ – Museum of Comparative Zoology, Harvard University; MOR – Museum of the Rockies; MWC – Museum of Western Colorado; NMMNH – New Mexico Museum of Natural History; SDSM – Museum of Geology, South Dakota School of Mines & Technology; TM – Tate Museum; UCM – University of Colorado Museum; USNM – National Museum of Natural History; UUVP – Utah Museum of Natural History (also UMNH); UW – Collection of Fossil Vertebrates, University of Wyoming; and YPM – Yale Peabody Museum.

QUARRIES

After more than 120 field seasons of crews working in the Morrison Formation, quite a few specimens and a lot of information have been collected. The quarries from which data were collected for this study are listed in Table 4.

The most diverse, productive, and/or stratigraph-ically important localities are described in detail in the following sections.

TABLE 4. List of Morrison Formation quarries from which data were taken for this study.

State	County	Locality Name	Key References
AZ	Navajo	Piñon Locality	Curtice, 1999
CO	Delta	Young Locality	Young, 1991
CO	El Paso	Garden of the Gods	Bakker, 1998
CO	Fremont	Cleveland Quarry	McIntosh & Williams, 1988
CO	Fremont	Clevlend II	—
CO	Fremont	Cope's Nipple	Osborn & Mook, 1921
CO	Fremont	Cope Quarry 8 (The Fort)	Carpenter, 1998a
CO	Fremont	Cope Quarry 12	Carpenter, 1998a
CO	Fremont	Cope's Lost Localities	Carpenter, 1998a
CO	Fremont	DeWeese Quarry	—
CO	Fremont	Egg Gulch	Carpenter, 1998a
CO	Fremont	Eric's Tooth	—
CO	Fremont	Felch Quarry II	Carpenter, 1998a
CO	Fremont	Garden Park General	—
CO	Fremont	Green Acres General	Carpenter, 1998a
CO	Fremont	Greg's Bone	Carpenter, 1998a
CO	Fremont	Jennings & Johnson	Ague et al. 1994
CO	Fremont	Kenny's *Stegosaurus*	Carpenter, 1998a
CO	Fremont	Kessler Quarry	Carpenter, 1998a
CO	Fremont	Lindsey Quarry	Carpenter, 1998a
CO	Fremont	Lucas' Site	Carpenter, 1998a
CO	Fremont	Marsh-Felch Quarry	Ostrom & McIntosh, 1966; Carpenter, 1998a
CO	Fremont	Meyer Site 1	Carpenter, 1998a
CO	Fremont	Meyer Site 2	Carpenter, 1998a
CO	Fremont	Meyer Site 3	Carpenter, 1998a
CO	Fremont	Meyer's Pump House	—
CO	Fremont	Sauropod Quarry	Carpenter, 1998a
CO	Fremont	Small Quarry	Carpenter, 1998a
CO	Fremont	Tim's Egg Site	Carpenter, 1998a
CO	Fremont	Valley of Death	Carpenter, 1998a
CO	Fremont	Wilson Creek	McIntosh, 1981
CO	Grand	Middle Park	—
CO	Grand	Radium Locality	—
CO	Gunnison	Cabin Creek Quarry	Bartleson & Jensen, 1988
CO	Gunnison	Blue Mesa Quarry	Fiorillo & May, 1996
CO	Jefferson	Interstate 70 Roadcut	—
CO	Jefferson	Lakes Morrison Q1	Ostrom & McIntosh, 1966
CO	Jefferson	Lakes Morrison Q5	Ostrom & McIntosh, 1966
CO	Jefferson	Lakes Morrison Q8	Ostrom & McIntosh, 1966
CO	Jefferson	Lakes Morrison Q10	Ostrom & McIntosh, 1966
CO	Larimer	Horsetooth Quarry	—
CO	Larimer	Masonville Locality	Bakker et al., 1990
CO	Las Animas	Purgatoire River	Lockley et al., 1986
CO	Las Animas	Villegreen	—
CO	Mesa	Bollan Quarry	Bollan, 1991
CO	Mesa	BYU Cactus Park	—
CO	Mesa	Hups Quarry	Kirkland et al., 1998
CO	Mesa	CU-Denver 3A	—
CO	Mesa	Dominguez-Jones	McIntosh et al., 1996
CO	Mesa	Dry Mesa Quarry	Britt, 1991; Curtice & Wilhite, 1996
CO	Mesa	Eriksen Ceratosaur	—
CO	Mesa	Fruita General	Callison, 1987
CO	Mesa	Fruita Main (Quarry 4)	Callison, 1987; Clark, 1985
CO	Mesa	Fruita Tom's Place	Callison, 1987
CO	Mesa	Fruita Quarry 2	—
CO	Mesa	Fruita Quarry 6	—
CO	Mesa	Fruita CTC	—
CO	Mesa	Fruita Little Blue	—
CO	Mesa	Fruita Mammal	—
CO	Mesa	Fruita Stego	—
CO	Mesa	Holt Quarry	Chenoweth, 1987b
CO	Mesa	Jones Hole	—
CO	Mesa	Koizumi Allosaur	—
CO	Mesa	Liz's Camarasaur	—
CO	Mesa	Mygatt-Moore Quarry	Kirkland & Carpenter, 1994
CO	Mesa	Rabbit Valley AMNH	—
CO	Mesa	Rabbit Valley East	—
CO	Mesa	Rabbit Valley Iguano	Armstrong & McReynolds, 1987; Bakker,1998

TABLE 4. (Continued)

State	County	Locality Name	Key References
CO	Mesa	Rabbit Valley Nest	—
CO	Mesa	Riggs Quarry 12	Chenoweth, 1991
CO	Mesa	Riggs Quarry 13	Riggs, 1903
CO	Mesa	Riggs Quarry 14	Chenoweth, 1991
CO	Mesa	Riggs Quarry 15	Chenoweth, 1987b
CO	Mesa	Split Rock 1	—
CO	Mesa	Split Rock 2	—
CO	Mesa	Wolny Site	Armstrong & McReynolds, 1987
CO	Moffat	Calico Gulch	Jensen, 1987
CO	Moffat	DNM Headquarters	—
CO	Moffat	Homestead Quarry	Chure et al., 1997
CO	Moffat	Lily Park	Shepard et al., 1977
CO	Moffat	MF Amphitheater	—
CO	Moffat	Witherell Quarry	—
CO	Moffat	Wolf Creek Quarry	Wood, 1986; Lederer & Small, 1999
CO	Montezuma	McElmo Canyon	—
CO	Montezuma	Yellowjacket Canyon	—
CO	Montrose	Potter Creek Quarry	Jensen, 1987
CO	Montrose	Scheetz Quarry	Scheetz, 1991; Kirkland, 1994
CO	Park	Webster Park	Madsen et al., 1995
CO	Saguache	Los Ochos Mine	—
CO	Summit	Heeney Site	—
MT	Big Horn	Horse Coulee/Beauvais	Mook, 1917
MT	Carbon	Mothers Day Quarry	—
MT	Gallatin	T&J Quarry	—
MT	Park	Strickland Creek	Wilson & Smith, 1996
MT	Wheatland	Wittecombe's Ranch	McIntosh, 1981
NM	Bernalillo	Peterson Quarry	Heckert et al., 2000; Williamson & Chure, 1996
NM	Cibola	Acoma Site	Lucas & Hunt, 1985
NM	Cibola	Boney Canyon NE	—
NM	Cibola	Concho Springs	Hunt & Lucas, 1993
NM	Cibola	Suwanee Peak	Lucas & Hunt, 1985
NM	Guadalupe	Bull Canyon	Lucas et al., 1985
NM	McKinley	Blue Peak	Lucas & Hunt, 1985
NM	Quay	Quay Localities	Hunt & Lucas, 1993
NM	Sandoval	Hagan Basin	Hunt & Lucas, 1993
NM	Sandoval	San Ysidro 1	Rigby, 1982
NM	Sandoval	San Ysidro 2	Hunt & Lucas, 1993
NM	Sandoval	*Seismosaurus* Quarry	Gillette, 1991; Schwartz & Manley, 1992
NM	Union	Exter	Lucas & Hunt, 1985
OK	Cimarron	Stovall Quarry 1	Stovall, 1938
OK	Cimarron	Stovall Quarry 3A	Hunt & Lucas, 1987
OK	Cimarron	Stovall Quarry 5	Hunt & Lucas, 1987
OK	Cimarron	Stovall Quarry 6	Hunt & Lucas, 1987
OK	Cimarron	Stovall Quarry 8	Mook, 1964
OK	Cimarron	Stovall Quarry 9	Hunt& Lucas, 1987
SD	Fall River	Parker's Mystery	Foster, 1996b
SD	Lawrence	Fuller's 351	Foster, 1996a, 1996b
SD	Meade	AMNH Quarry 1	—
SD	Meade	AMNH Quarry 2	—
SD	Meade	Bear Butte	Foster, 1996b
SD	Meade	North of Piedmont	Pinsof, 1983
SD	Meade	Piedmont Butte	Lull, 1919
SD	Meade	USNM Quarry	—
SD	Meade	Wonderland North	Foster, 1996a
SD	Meade	Wonderland Quarry	Foster, 1996a, 1996b
UT	Emery	Afton Nelson	—
UT	Emery	Agate Basin	—
UT	Emery	Cleveland-Lloyd Quarry	Miller et al., 1996; Madsen, 1976a
UT	Emery	CL Area Quarry 2	—
UT	Emery	CL Area Quarry 5	—
UT	Emery	CL Area Quarry 15	—
UT	Emery	CL Area Quarry 23	—
UT	Emery	CL Area Quarry 67	—
UT	Emery	Duke Site	—
UT	Emery	Ferron Quarry	—
UT	Emery	Green River Quarry	Kolb et al., 1996
UT	Emery	Hatt Ranch	—
UT	Emery	Mussentuchit Quarry	—

Colorado

Fruita Paleontological Area – Quarry 4

This is the main microvertebrate quarry in the Fruita, Colorado, area (Fig. 7). The site is in the middle of the formation near the base of the Brushy Basin Member and apparently is in an overbank splay deposit (Kirkland et al., 1990). The site has produced many specimens of a number of taxa, mostly microvertebrates, including the type of "*Fruitachampsa callisoni*," a small, gracile, terrestrial crocodilian, and several lizards and mammals.

Fruita Paleontological Area – Tom's Place

This is another relatively large quarry at Fruita and is at a similar stratigraphic level and in a similar paleoenvironment as Quarry 4. The quarry is in mudstone laterally adjacent to a sandstone bed and has produced numerous microvertebrate remains. This site and Quarry 4 contain a relatively diverse assemblage of lizard remains, including *Dorsetisaurus*, *Parviraptor*, *Saurillodon*, and *Paramacellodus*.

Cleveland Quarry

Ed Delfs and a crew from the Cleveland Museum of Natu-

TABLE 4. (Continued)

State	County	Locality Name	Key References
UT	Emery	San Rafael	—
UT	Emery	Sand Bench	Turner & Peterson, 1999
UT	Emery	66 Quarry	—
UT	Emery	Willow Springs Quarry	Galton, 1983
UT	Emery	Peterson Site	—
UT	Grand	Cisco	—
UT	Grand	Floy Junction	—
UT	Grand	Mill Canyon Quarry	Turner & Peterson, 1999
UT	Grand	Westwater	—
UT	San Juan	East Canyon Quarry	Gillette, 1996a, 1996b
UT	Uintah	Chevrons North	—
UT	Uintah	Chevrons South	—
UT	Uintah	Dinosaur Nat'l Mon. Quarry	McIntosh, 1981; Lawton, 1977
UT	Uintah	DNM *Apatosaurus*	—
UT	Uintah	DNM 15	—
UT	Uintah	DNM 2	—
UT	Uintah	DNM 375	Evans & Chure, 1998; Evans, 1999
UT	Uintah	DNM Miscellaneous	—
UT	Uintah	Rainbow Park 94	Chure, 1994
UT	Uintah	Rainbow Park 96	Chure & Engelmann, 1989
UT	Uintah	Soft Sauropod	—
UT	Uintah	Douglass Draw	—
UT	Uintah	Nielsen Draw	Gilmore, 1926
UT	Uintah	DNM 116	—
UT	Uintah	DNM Marsho	—
UT	Uintah	Jensen-Jensen Quarry	Jensen, 1987
UT	Uintah	Utah Field House Quarry	—
UT	Wayne	Hanksville Quarry	—
WY	Albany	AMNH 222 Quarry	—
WY	Albany	AMNH 223 Quarry	—
WY	Albany	AMNH 550 Quarry	—
WY	Albany	Bernice Quarry	—
WY	Albany	Bertha Quarry	Filla & Redman, 1994
WY	Albany	Bone Cabin Quarry	Osborn, 1903a
WY	Albany	Boris Quarry	—
WY	Albany	Breakfast Bench	Bakker et al., 1990
WY	Albany	Brown's Quarry A	Ostrom & McIntosh, 1966
WY	Albany	Brown's Quarry B	Ostrom & McIntosh, 1966
WY	Albany	Brown's Quarry C	Gilmore, 1920
WY	Albany	Brown's Quarry D	Ostrom & McIntosh, 1966
WY	Albany	Brown's Quarry G	Ostrom & McIntosh, 1966
WY	Albany	Cam Bench Quarry	Bakker, 1986
WY	Albany	Cam 1993	—
WY	Albany	Cassiopeia Quarry	—
WY	Albany	Convention Site	—
WY	Albany	Dead Rabbit Hill	Prothero, 1981
WY	Albany	Delta T	Prothero, 1981
WY	Albany	Drinker Quarry	—
WY	Albany	E. P. Thompson	Turner & Peterson, 1999
WY	Albany	Haystack Quarry	—
WY	Albany	Jeff P Quarry	—
WY	Albany	Louise Quarry	—
WY	Albany	Mummy Quarry	—
WY	Albany	Nail Quarry	Bakker, 1996
WY	Albany	Okie Quarry	—
WY	Albany	Pat M Quarry	—
WY	Albany	Reed's Quarry 1	Ostrom & McIntosh, 1966
WY	Albany	Reed's Quarry 2	Ostrom & McIntosh, 1966
WY	Albany	Reed's Quarry 3	Ostrom & McIntosh, 1966
WY	Albany	Reed's Quarry 4	Ostrom & McIntosh, 1966
WY	Albany	Reed's Quarry 6	Ostrom & McIntosh, 1966
WY	Albany	Reed's Quarry 8	Ostrom & McIntosh, 1966
WY	Albany	Reed's Quarry 9	Ostrom & McIntosh, 1966
WY	Albany	Reed's Quarry 10	Ostrom & McIntosh, 1966
WY	Albany	Reed's Quarry 11	Ostrom & McIntosh, 1966
WY	Albany	Reed's Quarry 13	Ostrom & McIntosh, 1966
WY	Albany	Reed's Quarry 14	Ostrom & McIntosh, 1966
WY	Albany	Reed's Quarry R	Chure & Fiorillo, 1997
WY	Albany	Regina Quarry	—
WY	Albany	Sheep Creek Quarry D(3)	Hatcher, 1901; McIntosh, 1981

TABLE 4. (Continued)

State	County	Locality Name	Key References
WY	Albany	Sheep Creek Quarry C	McIntosh, 1981
WY	Albany	Sheep Creek Quarry D	McIntosh, 1981
WY	Albany	Sheep Creek Quarry E	McIntosh, 1981
WY	Albany	Sheep Creek Quarry F	McIntosh, 1981
WY	Albany	Sheep Creek Quarry G	McIntosh, 1981
WY	Albany	Sheep Creek Quarry J	McIntosh, 1981
WY	Albany	Sheep Creek Quarry K	McIntosh, 1981
WY	Albany	Sheep Creek Quarry 4	McIntosh, 1981
WY	Albany	Stego 99	Schmude & Weege, 1996
WY	Albany	Two Thigh Quarry East	—
WY	Albany	Weege Boys Quarry	Schmude & Weege, 1996
WY	Albany	Zane Quarry	—
WY	Albany/Carbon	Como General	—
WY	Albany/Carbon	Cope's Como Quarry 1	—
WY	Albany/Carbon	Cope's Como Quarry 3	—
WY	Albany/Carbon	Cope's Como Quarry 4	—
WY	Albany/Carbon	Cope's Como Quarry 5	—
WY	Big Horn	Big Al Quarry	Breithaupt, 1996
WY	Big Horn	Big Butte Quarry	—
WY	Big Horn	Howe Quarry	Brown, 1935; Bird, 1985
WY	Big Horn	Little Butte	—
WY	Big Horn	Smithsonian Quarry 1	—
WY	Carbon	Beer Mug Locality	—
WY	Carbon	Chuck's Prospect	Prothero, 1981
WY	Carbon	Dryolestes Site	—
WY	Carbon	Dyer Ranch Q's 1 and 2	McIntosh, 1981
WY	Carbon	Freezeout Hills General	—
WY	Carbon	Freezeout Hills Quarry 4	—
WY	Carbon	Freezeout Hills Quarry 6	—
WY	Carbon	Freezeout Hills Quarry L	McIntosh, 1981
WY	Carbon	Freezeout Hills Quarry N	McIntosh, 1981
WY	Carbon	Freezeout Hills Quarry O	McIntosh, 1981
WY	Carbon	Lakes Quarry 1A	Ostrom & McIntosh, 1966
WY	Carbon	Meilyn Quarry	Schmude & Weege, 1996
WY	Carbon	Matt Quarry	Schmude & Weege, 1996
WY	Carbon	Ninemile Crossing	Dodson et al., 1980
WY	Carbon	Ninemile Hill	Trujillo, 1999
WY	Carbon	Reed's Quarry 1 1/2	Ostrom & McIntosh, 1966
WY	Carbon	Reed's Quarry 5	Ostrom & McIntosh, 1966
WY	Carbon	Reed's Quarry 7	Ostrom & McIntosh, 1966
WY	Carbon	Reed's Quarry 12	Ostrom & McIntosh, 1966
WY	Converse	Douglas Quarry	—
WY	Crook	Blacktail Creek	—
WY	Crook	Dillon's Corner	Foster, 1996a
WY	Crook	Hadley's Hill	Foster & Martin, 1994
WY	Crook	Lightning Rod Butte	Foster & Martin, 1994
WY	Crook	Little Houston Quarry	Foster & Martin, 1994; Foster, 2001
WY	Crook	MIA Locality	Foster, 1996a
WY	Crook	Mile 175	—
WY	Hot Springs	WSR BS Quarry	Bjoraker & Naus, 1996
WY	Hot Springs	WSR I Quarry	—
WY	Hot Springs	WSR RB Quarry	—
WY	Hot Springs	WSR BB Quarry	—
WY	Johnson	Buffalo Quarry	Carpenter & Miles, 1997; Carpenter et al., 2001
WY	Johnson	Elk Mountain	McIntosh, 1981
WY	Johnson	Poison Creek Quarry	Erickson, 1988
WY	Johnson	Red Fork Powder R. QA	McIntosh, 1981
WY	Johnson	Red Fork Powder R. QB	McIntosh, 1981
WY	Johnson	Sheridan College Allo Q	Flynn et al., 1997
WY	Johnson	Sheridan College Q1	—
WY	Johnson	Sheridan College Q2	—
WY	Natrona	Allen's Allo	—
WY	Natrona	Cottonwood Creek 1	—
WY	Natrona	Cottonwood Creek 2	—
WY	Natrona	Cottonwood Creek 3	—
WY	Natrona	Reed's Alcova Quarry	Gilmore, 1914
WY	Niobrara	Lance Creek	McIntosh et al., 1992
WY	Park	Paint Creek	—
WY	Weston	KU Quarry	—

ral History collected material from low in the Morrison at this site along Fourmile Creek in the Garden Park area north of Cañon City in the 1950s. In addition to the main sauropod skeleton (CMNH 10380), which McIntosh and Williams (1988) identified as the new species *Haplocanthosaurus delfsi*, there is the new crocodilian *Eutretauranosuchus delfsi* (Mook, 1967) and the turtle *Glyptops plicatulus*, as well as theropod teeth. The site is low in the formation in an overbank sandstone deposit.

Cope's Nipple

This site, quite high in the Morrison, was among the first sites collected in the Morrison Formation in the Garden Park area in 1877. Collectors working for E. D. Cope worked here for several years. Numerous pits in the vicinity have all been included in this one site (Carpenter, 1998a). This site, or set of pits, has produced the type specimens of *Camarasaurus supremus* and *Epanterias amplexus*. In addition, specimens of *Allosaurus*, *Apatosaurus*, *Stegosaurus*, *Goniopholis*, and *Glyptops* were found. The matrix at the site is reddish claystone interpreted as being deposited in a well-drained floodplain (Dodson et al., 1980).

Cope Quarry 8

This is another site high in the Morrison at Garden Park (Fig. 8), not far from Cope's Nipple (Carpenter, 1998a). The quarry

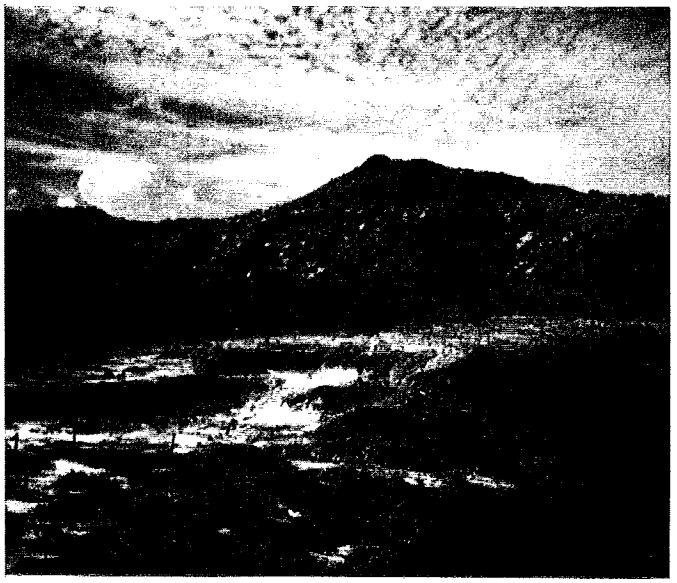

FIGURE 7. One of the microvertebrate quarries (left foreground) at the Fruita Paleontological Area, Colorado.

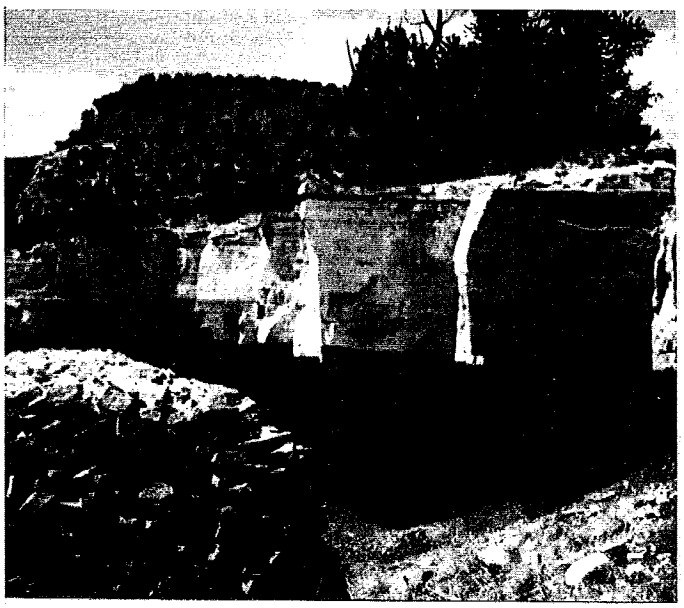

FIGURE 8. One of E.D. Cope's *Camarasaurus supremus* quarries from high in the Morrison Formation at Garden Park, Colorado.

has produced one individual of *Camarasaurus supremus*.

Cope Quarry 12

This locality has not been located with certainty, but it is known to be in the vicinity of Cope's Nipple and high in the formation. It produced the type specimen of *Amphicoelias altus* (AMNH 5764).

DeWeese Quarry

A specimen of *Diplodocus longus* (DMNH 462) was collected at this site in an area known as Green Acres on the eastern side of Garden Park during the winter of 1915–16. The site is in the upper middle part of the formation in smectitic, gray mudstone. A theropod tooth was found along with the main skeleton, and in 1997 a survey of the locality produced *Glyptops* shell fragments and a piece of goniopholid crocodilian skull and scutes.

Jennings and Johnson

This site, high in the Morrison at Garden Park near Cope's quarries, produced the holotype and only specimen of *Hallopus victor* (Marsh, 1877a). There has been some debate as to exactly what *H. victor* is and from what stratigraphic level it came, but Walker (1970) argued that it is most likely a small terrestrial crocodilian, and Ague et al. (1995) determined the stratigraphic level as being in the upper Morrison.

Kessler Quarry

This site was collected in the 1930s and is on the east side of Garden Park. It is relatively low in the formation and produced the mounted adult specimen of *Stegosaurus stenops* that is in the Denver Museum of Nature and Science (DMNH 1483), as well as *Allosaurus, Glyptops, Goniopholis*, ornithopod, and small theropod remains. The site is in a gray-green claystone.

Lindsey Quarry

This site is in eastern Garden Park and is in the upper middle part of the Morrison in pale green siltstone, though some large elements were in golden sandstone. A variety of taxa were found including *Camarasaurus, Allosaurus*, and *Glyptops*, together with some microvertebrates, including an anuran, a sphenodontid, and a fish.

Marsh-Felch Quarry

This site in the lower middle part of the Morrison was the main quarry collected for O.C. Marsh in the Garden Park area (Fig. 9). It was later worked by J.B. Hatcher for the Carnegie Museum (Evanoff and Carpenter, 1998a). The quarry is in a fluvial channel sandstone bed with well-displayed, underlying lateral accretion surfaces. A diverse fauna was found here, including the holotypes of *Diplodocus longus, Haplocanthosaurus priscus, Ceratosaurus nasicornis*, and *Kepolestes coloradensis*.

Sauropod Quarry

This site in the western part of Garden Park was worked by the Denver Museum of Nature and Science (Carpenter, 1998a) and is one of the stratigraphically lowest quarries in the Morrison

FIGURE 9. The Marsh-Felch Quarry at Garden Park, Colorado. The quarry is at the top of the channel sandstone unit in the center of the photograph.

(Turner and Peterson, 1999). It produced a specimen identified as *Haplocanthosaurus*, as well as turtle and theropod elements. The site is in a gray-green claystone.

Small Quarry

This quarry is one of the richest in the Garden Park area and is in the upper middle part of the Morrison. The deposit seems to have been an overbank pond that experienced occasional input of channel splays (Small and Carpenter, 1997). The main skeleton at the site was a nearly complete, articulated *Stegosaurus stenops*. Also found was the type specimen of the large pterodactyloid *Kepodactylus insperatus* (Harris and Carpenter, 1996), several other dinosaur taxa including the rare theropod *Elaphrosaurus* (Chure, 2001), and a significant microfauna, including several jaws of *Docodon* and a dryolestid.

Garden of the Gods

This site was near Colorado Springs somewhere within present-day Garden of the Gods State Park. A large camptosaurid skull was collected for O.C. Marsh here in the 1800s and is cataloged in the collections of the Yale Peabody Museum (Bakker, 1998).

Cabin Creek Quarry

A partial *Apatosaurus* was found at this site in the lower part of the Morrison near Gunnison, Colorado (Bartleson and Jensen, 1988).

Blue Mesa Quarry

This locality is on the north shore of Blue Mesa Reservoir west of Gunnison and has produced an *Apatosaurus* skeleton as well as a microvertebrate limb element and crocodilian and theropod teeth. The site appears to represent an overbank pond deposit next to a fluvial channel (Fiorillo and May, 1996). The stratigraphic position of the quarry is difficult to determine, as the lower part of the formation is under water.

Lakes Quarry 1 at Morrison

This was one of the first localities worked in the Morrison Formation and is along the hogback north of Morrison, Colorado, and just south of the Interstate 70 roadcut. The site was found by Arthur Lakes and Henry Beckwith in March of 1877 (see Ostrom and McIntosh, 1966; Kohl and McIntosh, 1997). The quarry is in a sandstone bed in the upper middle part of the formation; specimens of *Apatosaurus* and *Allosaurus*, as well as the type specimen of *Goniopholis felix* were collected from here.

Lakes Quarry 5 at Morrison

This is another of the sites Arthur Lakes worked for O. C. Marsh. The quarry is in a sandstone unit in the upper middle part of the formation and produced the type specimen of *Stegosaurus armatus* (Carpenter and Galton, 2001) and teeth assigned to *Diplodocus lacustris*, the latter of which could actually belong to any one of a number of diplodocids known from the formation.

Lakes Quarry 10 at Morrison

This quarry was just above the town of Morrison and produced bone from a black mudstone unit and an overlying sandstone bed. The quarry level is in the upper middle section of the Morrison Formation and produced several large *Apatosaurus* specimens, including *A. ajax* (YPM 1860), *Allosaurus*, and unidentified turtle remains.

Bollan Quarry

A partial skeleton of a *Stegosaurus* (MWC 81) was found in a sandstone at this site west of Grand Junction in 1978 (Bollan, 1991). The site is in the upper middle part of the formation (Armstrong and McReynolds, 1987; Turner and Peterson, 1999).

Cactus Park BYU Quarry

This site, on the eastern edge of the Uncompahgre Plateau south of Grand Junction, was worked by Jim Jensen, and the material from it is at the BYU Earth Science Museum. Several individuals of *Apatosaurus* and *Camarasaurus* were found here and many of the elements were of juveniles (Curtice and Wilhite, 1996).

Hups Quarry

This site, in the upper middle part of the Morrison Formation at Cactus Park, was found by Kent Hups of the University of Colorado at Denver. It produced a partial skeleton of *Mymoorapelta* (MWC 2610) (Kirkland et al., 1998) and a partial gonipholid crocodilian, as well as elements of *Allosaurus*. The specimens are in a hard, well-cemented sandstone bed that has slowed their preparation.

Dominguez-Jones Quarry

This site was worked by Jim Jensen and produced the type and only specimen of the sauropod species *Camarasaurus lewisi* (Jensen, 1988; McIntosh et al., 1996). The quarry is on the east slope of the Uncompahgre Plateau and is near the middle of the formation.

Dry Mesa Quarry

This is one of the most important quarries in the Morrison Formation in terms of both diversity and numbers of specimens collected. Excavated since 1972 by Jim Jensen and/or crews from the BYU Earth Science Museum, the Dry Mesa Quarry is in the lower middle part of the Morrison near the base of the Brushy Basin Member and is in medium-grained to gravelly sandstone. The site has produced most of the known major genera of Morrison dinosaurs, plus the type specimens of *Torvosaurus tanneri*, *Supersaurus vivianae*, *Dystylosaurus edwini*, and the pterosaur *Mesadactylus ornithosphyos* (Galton and Jensen, 1979; Jensen, 1985; Chenoweth, 1987a; Jensen and Padian, 1989; Britt, 1991; Miller et al., 1991). The type of *Ultrasauros macintoshi* appears not even to be brachiosaurid and may even belong to *Supersaurus*, and the scapula referred to *Ultrasauros* has now been referred to *Brachiosaurus* (Curtice et al., 1996). Also, the site contains remains of a number of smaller vertebrates, including a mammal, juvenile sauropods, and even an embryonic camarasaurid (Prothero and Jensen, 1983; Jensen and Padian, 1989; Britt and Naylor, 1994; Curtice and Wilhite, 1996). Morris et al. (1996) interpreted the Dry Mesa deposit as that of a shallow but wide braided stream, with bones deposited during relatively rapid flood stage flow.

Mygatt-Moore Quarry

This site, just north of Interstate 70 and several miles from the Utah border, has produced a number of taxa, including the type specimen of *Mymoorapelta maysi*, the first known North American Jurassic ankylosaur (Kirkland and Carpenter, 1994) as well as several nearly complete fish (Kirkland, 1998). Most of the dinosaur material pertains to *Apatosaurus*, *Camarasaurus*, and *Allosaurus*. The quarry is in the upper middle part of the formation and is in gray silty claystone that may represent a pond deposit (Kirkland and Armstrong, 1992).

Riggs Quarry 12

This site is just east of Colorado National Monument south of Grand Junction and produced a *Camarasaurus* specimen (Chenoweth, 1991).

Riggs Quarry 13 (Riggs Hill)

This site is just southwest of Grand Junction and was found on July 4, 1900 (Chenoweth, 1987b). The quarry produced the type specimen of *Brachiosaurus altithorax* (FMNH 25107; Riggs, 1903) and is in the middle of the formation in a sandstone unit.

Riggs Quarry 14

This site near Fruita produced a *Camarasaurus* specimen (Chenoweth, 1991). The exact location of the quarry has not been determined.

Riggs Quarry 15 (Dinosaur Hill)

This site is in the Brushy Basin Member just south of Fruita, Colorado, and produced the *Apatosaurus* specimen that is mounted in the Field Museum of Natural History in Chicago (Chenoweth, 1987b). The quarry is in a reddish mudstone representing a well-drained floodplain (Dodson et al., 1980).

Homestead Quarry

This site southeast of Dinosaur National Monument has produced a partial skeleton of *Marshosaurus bicentessimus*, along with parts of the ornithopod *Dryosaurus* and the crocodilian *Goniopholis*. The site is in an overbank unit consisting of interbedded siltstones and sandstones.

Lily Park

This locality was found in 1955 and produced an articulated skeleton of *Dryosaurus altus* (Shepherd et al., 1977; McIntosh, 1981). A nearby site produced a claw of *Torvosaurus tanneri* (Galton and Jensen, 1979; McIntosh, 1981).

Witherell Quarry

This site is a private quarry near the Skull Creek drainage east of Dinosaur, Colorado. The site is in mudstone and has produced remains of the sauropod *Camarasaurus*, the lungfish *Ceratodus*, theropods, and crocodilians, as well as an articulated individual of *Othnielia*. Another site in a nearby sandstone produced a partial theropod skeleton.

Wolf Creek Quarry

The Wolf Creek Quarry is north of Massadona and was found in 1979 by India Wood, who at the time was just 13 years old. She worked the site with crews from the Denver Museum of Natural History in the early 1980s and returned to work a microvertebrate layer at the site in 1985 with two fellow Dartmouth undergraduates (Wood, 1986). The material from the site is in the collections of the DMNH and the Museum of Comparative Zoology at Harvard University and includes the *Allosaurus* now mounted in the Denver Museum of Nature and Science (DMNH 2149) and a partial *Stegosaurus* skeleton (DMNH 2150). At least 12 other taxa are known from the site, including salamander and frog elements, sphenodontian jaw fragments, a mammalian humerus, and a lizard jaw fragment. The quarry occurs in silty gray claystone and is in the lower middle part of the formation.

Potter Creek Quarry

This quarry was found in 1943 by Eddie and Vivian Jones and was worked by Jim Jensen. It produced a partial skeleton of *Brachiosaurus* as well as theropod teeth (Jensen, 1987).

Scheetz Locality

This site is southwest of Uravan and has been surface collected and screenwashed. The locality has produced more than two thousand bone fragments that appear to represent at least eight individuals of *Dryosaurus* that are baby- and juvenile-sized (Scheetz, 1991). The site has also produced remains of turtles, a pterosaur, fish, theropods, sauropods, goniopholid crocodilians, sphenodontids, and a multituberculate mammal (Scheetz, 1991; Kirkland, 1994). The locality is in the lower middle part of the Morrison in a mudstone bed.

Montana

Horse Coulee/Beauvais Creek

This site has been referred to by two different names by Mook (1917) and in the records of the AMNH, respectively, but both list the location as "30 mi east of Pryor" in Montana, so they are likely the same locality. Fred Peterson and Christine Turner (pers. comm., 1997) have tried unsuccessfully to relocate the quarry. *Camarasaurus* and *Diplodocus* remains have been collected here.

Strickland Creek Quarry

This quarry is in sandstone and has produced turtle, *Allosaurus*, and *Diplodocus* remains, as well as those of a sauropod that has been referred to *Amphicoelias* (Wilson and Smith, 1996).

Wittecombe's Ranch

The material from this locality is in the Carnegie Museum and includes *Camarasaurus*, *Diplodocus*, *Goniopholis*, *Ceratodus*, *Allosaurus*, *Stegosaurus*, and turtle (McIntosh, 1981; pers. obs.).

New Mexico

Peterson Quarry

This locality occurs near the upper middle part of the formation in coarse-grained sandstone and has produced specimens of *Camarasaurus*, a diplodocid, and a large allosaurid (Williamson and Chure, 1996; Heckert et al., 2000). The allosaurid is a partial, articulated skeleton and may be *Allosaurus* or, less likely, *Saurophaganax*.

Concho Springs

Occuring in the middle of the formation, this locality is in light green and maroon claystone and produced *Stegosaurus* remains (Chenoweth, 1953; Lucas and Hunt, 1985; Hunt and Lucas, 1993).

Bull Canyon

This locality, low in the Morrison, has produced numerous fragmentary dinosaur remains; the only identifiable specimen is a caudal vertebra of *Stegosaurus* (Lucas et al., 1985).

Blue Peak

This site northeast of Grants in western New Mexico has produced a fragmentary, and now missing, specimen of *Apatosaurus* (Chenoweth, 1953; Lucas and Hunt, 1985; Hunt and Lucas, 1993).

San Ysidro 1

This locality is in the upper middle part of the Morrison and has produced a partial skeleton of *Camarasaurus supremus* (NMMNH 21094) and teeth of *Allosaurus* (Rigby, 1982; Lucas and Hunt, 1985; Lucas et al., 1985; Hunt and Lucas, 1993). The site is in a well-drained floodplain deposit.

San Ysidro 2

Hunt and Lucas (1993) mention a partial sauropod specimen from the San Ysidro area (NMMNH P-21095) that they identify as *Diplodocus carnegii*.

Seismosaurus Quarry

This locality was found by hikers in the late 1970s and was excavated in the 1980s. The site is in sandstone in the middle of the Morrison and produced a theropod tooth and the partial, articulated type specimen of the large sauropod *Seismosaurus hallorum* (Gillette, 1991; Schwartz and Manley, 1992).

Oklahoma

Stovall Quarry 1

This was the main quarry worked by J.W. Stovall, University of Oklahoma students, and Work Projects Administration crews in extreme northwestern Oklahoma in the 1930s and early 1940s (Fig. 10). First found in 1931 when a road construction crew hit the bone layer with a grader, the quarry produced specimens of *Apatosaurus*, *Camarasaurus*, *Stegosaurus*, and *Camptosaurus* (Stovall, 1938; Hunt and Lucas, 1987), as well as the type specimen of *Saurophaganax maximus* (Ray, 1941; Chure, 1995). Several of the sauropod specimens know from this quarry are very young juveniles and are among the smallest known individual sauropods in the Morrison (Carpenter and McIntosh, 1994). The quarry is in grayish green claystone just below a sandstone bed and is in the upper part of the formation. Due to a disasterous loss of data, it is now difficult, if not impossible, to ascertain which specimens came from which Stovall quarries (Hunt and Lucas, 1987).

Stovall Quarry 3A

This is a locality that produced a specimen of *Stegosaurus*. The site is in the middle of the formation in claystone (Hunt and Lucas, 1987).

Stovall Quarry 5

This site produced a large number of bones, very few of which were identifiable, but one string of seven articulated sauropod vertebrae was identified by Stovall as *Diplodocus* (Hunt and Lucas, 1987).

Stovall Quarry 6

This site was in the upper middle Morrison in claystone and produced a specimen of *Apatosaurus* (Hunt and Lucas, 1987).

Stovall Quarry 8

This quarry produced numerous turtle elements, some fish vertebrae and scales, and many elements of crocodilians, including about 300 skeletal elements and more than 1100 teeth (Hunt and Lucas, 1987). This collection of crocodilian remains may represent 70 or so individuals. In addition, the quarry produced two skulls of *Goniopholis*, one of which became the type of *G. stovalli* (Mook, 1964).

Stovall Quarry 9

Another locality in the upper middle Morrison that produced *Apatosaurus*, this site is in red claystone (Hunt and Lucas, 1987).

South Dakota

Fuller's 351

This quarry was found in 1935 and worked that summer (Bump, 1939). The locality is in the northern Black Hills northeast of Spearfish and occurs near the top of the formation in a light gray siltstone bed (Fig. 11). The site produced a number of bones, of which perhaps only half have been fully prepared. Present in the quarry are remains of one adult and one juvenile *Apatosaurus*, an *Allosaurus* (Bjork, 1983), and numerous elements of a fairly large, adult *Camarasaurus* skeleton (SDSM 351) (Foster, 1992, 1996a, 1996b).

Bear Butte

This site is near the top of the Morrison on the west slope of Bear Butte, northeast of Sturgis, in green-gray claystone. An anterior caudal and several other elements of an *Apatosaurus* were collected here in 1984 and are in a private collection.

North of Piedmont

A single specimen of *Ceratodus* was found in 1942, reportedly in the Morrison Formation (Pinsof, 1983). The site has not been relocated, but the specimen could be Jurassic in age.

Piedmont Butte

This quarry was first worked in 1889 by O. C. Marsh and J.

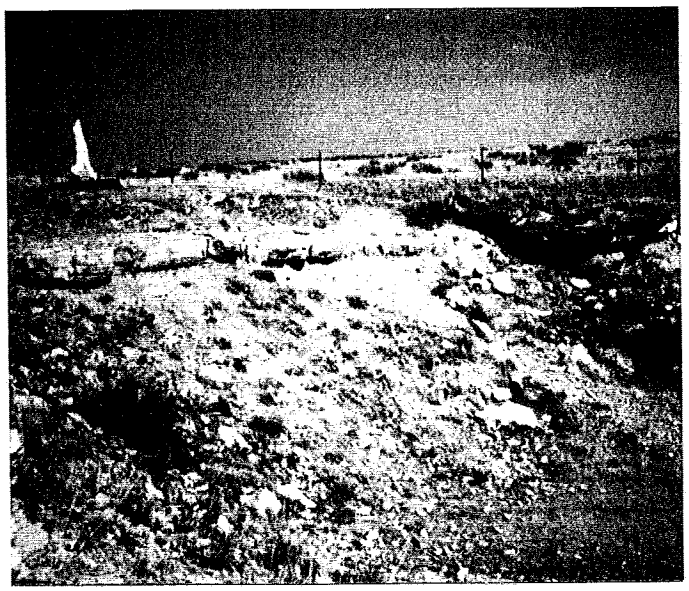

FIGURE 10. Stovall's Quarry 1 near Kenton, Oklahoma, type locality of the large allosaurid *Saurophaganax*.

FIGURE 11. The Fuller's 351 quarry near Spearfish, South Dakota. The pit is visible just below sandstones of the Lakota Formation.

B. Hatcher and is several miles north of Rapid City, just east of the town of Piedmont. Marsh and Hatcher recovered the initial elements (YPM 429) that became the type of the sauropod *Barosaurus lentus* (Marsh, 1890a). G. Wieland returned in 1898 to collect the remaining parts of the skeleton for Marsh (Wieland, 1920), and a full description of the specimen was published by Lull (1919). The quarry is in green-gray claystone several meters above the Unkpapa Sandstone Member of the Morrison Formation and also produced several theropod teeth and metatarsals of a smaller sauropod that Marsh (1890a) named *B. affinis*; the material of this species is diplodocid but is otherwise indeterminate.

Wonderland Quarry

This locality was found by G. Szigeti (1979) and worked by a crew from the South Dakota School of Mines in 1980. The site produced teeth of *Camarasaurus*, a metatarsal, caudal, and teeth of *Allosaurus*, numerous shell fragments of *Glyptops*, crocodilian teeth (Foster, 1992, 1996b), a *Cteniogenys* vertebra (Foster and Trujillo, 2000), and an ilium of a juvenile *Stokesosaurus* (Foster and Chure, 2000). The main skeleton at the quarry is a partial skeleton of *Barosaurus lentus* (SDSM 25210), which consists mainly of caudal vertebrae but also has several other incomplete elements (Foster, 1996a). The site is in a light gray silty claystone bed (Foster, 1992, 1996b).

Utah

Cleveland-Lloyd Quarry

This is one of the largest quarries in the Morrison in terms of numbers of elements found. The site is in the northwestern San Rafael Swell region, and the main bone layer is in gray claystone below a limestone bed and appears to represent a temporary or seasonal pond that became a predator trap (Stokes, 1985; Miller et al., 1996; Richmond and Morris, 1996). Of the nearly 70 individuals represented here, 44 belong to *Allosaurus* and represent a range of ages from very young juveniles up to adults (Madsen, 1976a). A number of other taxa are present as well, including the type specimens of *Stokesosaurus* (Madsen, 1974) and *Marshosaurus* (Madsen, 1976b) and a new species of *Ceratosaurus* (Madsen and Welles, 2000). The quarry is in the upper middle part of the formation. Bones in the quarry are in most cases entirely disarticulated and, as there is little association of elements that may belong to one individual, appear to be scattered.

Ferron Quarry

This site, in the western San Rafael Swell, is east of the town of Ferron and is in a coarse-grained sandstone bed. An articulated partial skeleton of *Allosaurus* was found here recently and appears to be low in the Brushy Basin Member.

Green River Quarry

This locality just west of Green River produced an *Allosaurus* specimen from a gray claystone unit (Kolb et al., 1996).

Mussentuchit Quarry

This site is in the San Rafael Swell south of Interstate 70 and was worked by CEU crews. The site is in silty mudstone and produced *Camarasaurus*, *Allosaurus*, *Diplodocus*, and turtle and crocodilian remains.

Sand Bench

This site in the middle of the Morrison produced a specimen of *Ceratosaurus* (Turner and Peterson, 1999).

66 Quarry

This is a locality of the Prehistoric Museum at the College of Eastern Utah and has produced *Apatosaurus* and *Allosaurus*.

Willow Springs Quarry

This site is not too far from the Mussentuchit Quarry and produced an articulated partial skeleton of a juvenile *Allosaurus* (MCZ 3897) and an *Othnielia* (Galton, 1983). The *Allosaurus* specimen consists of a premaxilla, maxilla, three cervicals, 10 dorsal vertebrae, sacrum, ilia, several caudals, scapula, coracoid, phalanges, unguals, 11 ribs, pubes, ischia, femur, tibia, and fibula. The site was worked by Jim Jensen and is in tan siltstone.

Peterson Site

This locality is in a channel sandstone bed in the southwestern part of the San Rafael Swell and produced remains of a large megalosaurid, probably *Torvosaurus* (CEUM 330).

Mill Canyon Quarry

This quarry is northwest of Moab and was worked by crews from the BYU Earth Science Museum. It has produced *Camarasaurus*, *Allosaurus*, *Camptosaurus*, and *Stegosaurus* (Turner and Peterson, 1999).

East Canyon Quarry

This is one of the first sites found in the Jurassic of the western United States. The locality was found in 1859 during a western exporation survey by the Macomb Expedition, and some elements of a sauropod forelimb were collected. These were used as the basis for *Dystrophaeus viaemalae* (Cope, 1877c), probably the oldest known sauropod from North America (Gillette, 1996a,b) (but see Summerville Formation in Lucas et al., 1995). The site was relocated by Fran Barnes in 1989 and is in what appears to be an overbank sand deposit in the Tidwell Member of either the Morrison or Summerville Formation (Peterson and Turner-Peterson [1987] vs. Anderson and Lucas [1995]).

Carnegie Quarry, Dinosaur National Monument

This is one of the most important localities in the formation. A diverse assemblage of dinosaur taxa is found at the quarry, and the number of bones present in the deposit is one of the greatest in the Morrison. Found in 1909 by Earl Douglass and worked for a number of years, the quarry is in a sandstone ridge east of Vernal. It became a National Monument, and the remaining part of the quarry was covered with a quarry building and visitor center. The quarry bone deposit is in a gravelly channel sandstone and was probably deposited in as little as several years (Lawton, 1977; Fiorillo, 1994). Information on the taxa present and numbers of specimens came from Gilmore (1936), McIntosh (1981), and catalogs of Dinosaur National Monument and several museums. Most of the common dinosaurian genera of the Morrison Formation are present, and the quarry produced the type specimen of the turtle *Dinochelys whitei* (Gaffney, 1979). Articulated partial to nearly complete dinosaur skeletons are present as well as disarticulated elements; the sauropods *Diplodocus* and *Camarasaurus* are fairly common (Fig. 12). The site also produced remains of a juvenile *Stegosaurus* (Galton, 1982a).

Rainbow Park 94

This microvertebrate site in the northern part of Dinosaur National Monument has produced a diverse assemblage of animals including the type specimen of the theropod *Koparion douglassi* (Chure, 1994).

Rainbow Park 96

This is another site near Rainbow Park 94, within Dinosaur National Monument, that has produced partial pipoid frog skel-

FIGURE 12. Skull and cervical vertebrae of a *Camarasaurus* specimen at the Dinosaur National Monument quarry, Utah.

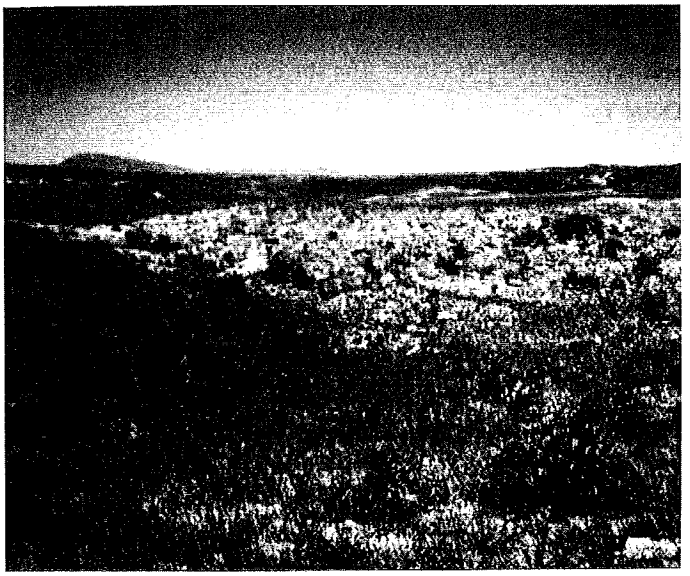

FIGURE 13. The historic Bone Cabin Quarry in Albany County, Wyoming, worked by the American Museum of Natural History.

etons (Henrici, 1997, 1998) and other microvertebrate material. Both localities 94 and 96 at Rainbow Park are high in the formation and occur in gray mudstone-siltstone units (Chure and Engelmann, 1989).

Douglass Draw Quarry

This locality high in the formation at Dinosaur National Monument produced a hatchling *Camptosaurus* specimen (Chure et al., 1994).

DNM 116

This is a site east of the main quarry that produced a nearly complete, articulated *Allosaurus* specimen with skull. The quarry is low in the formation and is in gravelly sandstone. The specimen probably represents a new species of *Allosaurus* (Chure, pers. com., 1997, 2002).

DNM *Marshosaurus*

Chure et al. (1997) mentioned a theropod specimen possibly referable to *Marshosaurus* from nearby the main DNM quarry building and at a lower level in the Brushy Basin Member.

DNM 375

A microvertebrate site within Dinosaur National Monument, this locality has yielded specimens of *Cteniogenys*, the new lizard *Schilleria*, and a partial articulated skeleton of a salamander.

Jensen-Jensen Quarry

This site, relatively low in the Morrison, was excavated by Jim Jensen and is across the Green River southeast of the Dinosaur National Monument quarry. The site is in a sandstone unit and produced *Brachiosaurus*, *Camarasaurus*, and *Apatosaurus* (Jensen, 1987).

Wyoming

Bertha Quarry

This site low in the Morrison in the eastern part of Como Bluff has produced the type specimen of *Apatosaurus yahnahpin* (Filla and Redman, 1994) and parts of a *Dryosaurus* and a goniopholid crocodilian. The site is in an overbank, near-channel mudstone bed and the main sauropod skeleton seems to be from an animal that became mired in the soft mud.

Bone Cabin Quarry

This locality is several miles north of Como Bluff and is in a channel sandstone bed (Fig. 13). The site was worked around the turn of the century by crews from the American Museum of Natural History (Osborn, 1904) and is worked currently by Western Paleontological Laboratories. Most of the main dinosaurian genera from the Morrison Formation have been found at this quarry, but it has also produced the type specimens of *Ornitholestes hermanni* (Osborn, 1903) and *Gargoyleosaurus parkpini* (Carpenter et al., 1998). Several juvenile dinosaur specimens are known, as well as two very young *Stegosaurus*. Non-dinosaurian taxa include the turtles *Dinochelys* and *Glyptops* and the crocodilian *Goniopholis*. Many bones were collected here, and the total minimum number of individuals represented is nearly 70.

Boris Quarry

This site in the Sheep Creek area yielded elements of *Apatosaurus* and *Allosaurus* as well as the posterior portion of an ankylosaur skull (UW 21869).

Breakfast Bench

This area in the eastern part of Como Bluff has produced a number of microvertebrate sites that have yielded crocodilian teeth, the large lungfish *Ceratodus robustus*, and the type specimens of the turtle *Uluops uluops*, the small ornithopod *Drinker nisti*, and the mammals *Foxraptor atrox* and *Zofiabaatar pulcher* (Bakker et al., 1990; Carpenter, 1998b). The site area is in a dark mudstone and appears to be part of a wet floodplain environment; it is also high in the Morrison.

Dead Rabbit Hill

This site is west of Quarry 9 along Como Bluff and was worked in the 1960s (Prothero, 1981). It produced the lungfish *Ceratodus*, the turtle *Glyptops*, and the mammal *Docodon* (AMNH 104799). The quarry is fairly low in the formation.

Ninemile Hill

This locality is in the upper part of the Morrison Formation (Trujillo, 1999) and has so far produced mostly microvertebrates including fish, crocodilian and turtle material, the lungfish

Ceratodus, *Cteniogenys* vertebrae, theropod teeth, salamander vertebrae, and the mammals *Docodon*, *Ctenacodon*, *Psalodon*, *Dryolestes*, and *Laolestes*, (Trujillo, 1999). The site is in a gray claystone.

Delta T

This locality is high in the formation near the upper contact and produced the lungfish *Ceratodus*, the turtle *Dinochelys*, the crocodilian *Goniopholis*, and a multituberculate (AMNH 101146). The site is near Quarry 9 (Prothero, 1981).

Nail Quarry

This is an important quarry near the middle of the formation (Turner and Peterson, 1999) that is in gray smectitic claystone with some limestone. The stratigraphic level has been referred to as the "Talking Rocks member" of the Morrison (Allen, 1996; Bakker, 1996). The site has produced a crocodilian and the dinosaurian genera *Allosaurus* (TM 0011), *Apatosaurus*, *Stegosaurus*, *Diplodocus*, and *Camarasaurus*. It has also produced the type specimen of the megalosaurid *Edmarka rex* (Bakker et al., 1992), which probably represents *Torvosaurus*.

Reed's Quarry 1

This Como Bluff locality was the first of a series of quarries found by W. H. Reed starting in 1877 and worked by him and others for O. C. Marsh. The quarry is in the upper middle part of the Morrison in claystone and has produced four adult and two juvenile individuals of *Camarasaurus grandis*, one *Diplodocus*, two *Allosaurus*, and an unidentifiable mammal tooth (Ostrom and McIntosh, 1966; Carpenter and McIntosh, 1994).

Reed's Quarry 3

This quarry was also in the upper part of the formation and produced five juvenile individuals of the sauropod *Camarasaurus grandis*, as well as *Allosaurus*, *Stegosaurus*, and *Dryosaurus* (Ostrom and McIntosh, 1966).

Reed's Quarry 4

This quarry was found in 1878 and produced several sauropod genera including *Barosaurus*, as well as *Allosaurus* and *Stegosaurus*. The quarry matrix was gray silty claystone.

Reed's Quarry 6

This is a site that produced a specimen of the crocodilian *Goniopholis*.

Reed's Quarry 8

This site is in the upper part of the formation and produced several genera of dinosaurs as well as *Goniopholis* and a turtle. The quarry is in pale gray to green-gray silty claystone with some carbonate and mud clasts.

Reed's Quarry 9

This locality, often referred to simply as Quarry 9, was found in July of 1879 and worked for nearly 10 years (Ostrom and McIntosh, 1966; Kohl and McIntosh, 1997) (Fig. 14). The quarry produced one of the most important collections of Mesozoic mammals in the world and also produced a wide assortment of other microvertebrates as well as a number of common dinosaurian genera (Simpson, 1926a, 1929; Ostrom and McIntosh, 1966; Lillegraven et al., 1979; Prothero, 1981). The site was worked by Marsh's crews from 1879 to around 1889, by the American Museum of Natural History under the direction of H. F. Osborn in 1897, in the early 1960s by Bill Turnbull of the Field Museum in Chicago, and in the late 1960s by an AMNH and Yale Peabody Museum expedition. The quarry is fairly high in the formation

FIGURE 14. Reed's Quarry 9 at Como Bluff, Wyoming. The quarry is in the center distance at the base of the bluff.

and produced microvertebrate remains from two layers, one above and one below a sandstone layer. The lower layer consists of green siltstone and sandstone and is the level worked by earlier expeditions, whereas the upper gray claystone layer was worked by the AMNH/YPM group (Prothero, 1981). Small bones in the deposit are relatively common and are disarticulated. The site produced numerous type specimens, particularly of mammals and other microvertebrates. In fact, a majority of the type specimens of mammals from the Morrison Formation come from this one quarry. Some of the still-valid taxa based on type specimens found here include: the frog *Ennaebatrachus*, the sphenodontians *Opisthias* and *Theretairus*, the choristodere *Cteniogenys*, the crocodilian *Macelognathus*, and many genera of mammals.

Reed's Quarry 10

This site is not far west of Quarry 9 and is at a similar stratigraphic level, though it is in a gray, smectitic claystone. The quarry produced a skeleton of the sauropod *Apatosaurus excelsus* (YPM 1980), which is now on display at the Yale Peabody Museum.

Reed's Quarry 11

This locality produced specimens of *Apatosaurus amplus*, *Stegosaurus*, and an unidentified mammal tooth. The quarry is in the upper middle part of the formation.

Reed's Quarry 13

This quarry is in fine-grained sandstone low in the Morrison at the eastern end of Como Bluff. The collection includes crocodilian and turtle material and several dinosaurs, including three individuals of the small theropod *Coelurus* (Ostrom, 1980b). Most of the material from this site is in the YPM and the National Museum of Natural History (USNM) and consists of dozens of disarticulated elements belonging to *Camptosaurus* and *Stegosaurus*. Both genera are represented by adults and juveniles, and considering all taxa, there are probably close to 40 individuals represented at the quarry.

Reed's Quarry 14

This locality in the upper middle part of the formation is in a gray siltstone bed and produced an *Allosaurus* specimen (YPM 1893).

Reed's Quarry R

This site is southeast of Como Bluff and was worked by Reed for the AMNH a number of years after his work for O. C. Marsh. The site produced a number of individuals of some fairly common dinosaurian genera. One specimen of *Allosaurus* from this locality has a set of large theropod tooth marks on the pubic bone, which led Chure and Fiorillo (1997) to speculate that the specimen had been fed on by *Torvosaurus* or *Ceratosaurus*.

Sheep Creek Quarry D(3)

This is one of several quarries worked around the turn of the century by crews from the Carnegie Museum in the Sheep Creek region north of Como Bluff (McIntosh, 1981). This site is near the middle of the formation and produced the holotype of *Diplodocus carnegii* (CM 84), together with remains of two other individuals of the species. Also in the collection are two individuals of *Stegosaurus*.

Sheep Creek Quarry C

This locality produced an *Apatosaurus* and an adult and juvenile *Camarasaurus* (McIntosh, 1981; Carpenter and McIntosh, 1994).

Sheep Creek Quarry D

A site near the middle of the formation, this quarry produced specimens of *Stegosaurus*, *Apatosaurus excelsus* (CM 555), and *Camarasaurus grandis*.

Sheep Creek Quarry E

This is a locality that produced specimens of *Stegosaurus* and *Camarasaurus*. It also is the quarry that yielded CM 563 (UW 15556), an *Apatosaurus excelsus* that is mounted at the University of Wyoming Geological Museum and CM 566, a very young *Apatosaurus excelsus* described by Peterson and Gilmore (1902).

Stego 99

This is an old locality that produced a *Stegosaurus* specimen from a sandstone bed fairly high in the formation (Dodson et al., 1980). Specimens of *Glyptops*, crocodilians, and theropods (mostly teeth) are in the collections of the MCZ.

Zane Quarry

This is another locality in the Sheep Creek area that has been worked by crews under R.T. Bakker. It is fairly low in the Morrison and produced *Camarasaurus*, *Apatosaurus*, *Diplodocus*, *Stegosaurus*, a theropod, and an ankylosaur.

Big Al Quarry

This site is on the east side of the Bighorn Basin in north-central Wyoming and produced a nearly complete, articulated, sub-adult *Allosaurus* from a sandstone bed in about the middle of the formation (Breithaupt, 1996). The specimen (MOR 693) has bone pathologies and shows evidence of having been scavenged by beetles before burial (Laws et al., 1996; Hanna, 2002).

Howe Quarry

This is a major quarry that was worked in the 1930s by crews from the American Museum of Natural History under the direction of Barnum Brown. The same bed has also been worked very close by in recent years (Siber, 1992). The quarry is on the east side of the Bighorn Basin north of Shell and is very close to the Big Al Quarry. The quarry is relatively low in the formation in a clay-siltstone bed between two sandstone units and produced several genera of dinosaurs (Brown, 1935); diplodocids appear to be particularly common and are represented by isolated elements and articulated limbs and series of vertebrae. Unfortunately, very little of the material from this site has been prepared, so few positive identifications can be made. One juvenile sauropod specimen has been identified as *Barosaurus*. The bone deposit is thick in the center and thins toward the edges, and close to a dozen dinosaur limbs were preserved articulated and upright (Farlow in Bird, 1985). The site appears to represent an overbank pond or mudhole in which at least several diplodocid individuals became trapped. The recent Siber excavation has produced associated skeletons of *Camarasaurus*, *Stegosaurus*, *Allosaurus*, *Dryosaurus*, and *Othnielia*, in addition to five individuals of *Diplodocus* (Siber and Siber, 1997). The site also yielded some of the few specimens of sauropod skin impressions known from the Morrison (Czerkas, 1992).

Freezeout Hills

Several localities were located in this area northwest of Como Bluff and worked by crews from the Carnegie Museum under Charles Gilmore (McIntosh, 1981) and from the Field Museum under Elmer Riggs. Most of the material from these sites belongs to fairly common dinosaur genera, but one caudal in the Field Museum collected by Riggs appears to belong to *Brachiosaurus* (Curtice, pers. comm., 1997). Also, microvertebrate material has been collected here by Anthony Fiorillo, and in the 1970s Ken Carpenter found a mammal tooth that is now in the University of Colorado Museum.

Lakes's Quarry 1A

This site at Como Bluff is in a medium-grained sandstone bed fairly low in the formation. The locality produced *Allosaurus*, *Camarasaurus*, *Camptosaurus*, and an as yet unprepared femur of a small ornithopod, probably *Othnielia*.

Meilyn Quarry

This is one of the lowest quarries in the Morrison and is north of Como Bluff. The quarry is in a sandstone bed and has produced an *Allosaurus* and a stegosaur (Schmude and Weege, 1996).

Nine Mile Crossing

This locality was found by AMNH crews north of Como Bluff and produced the skeleton of *Apatosaurus excelsus* (AMNH 460) now mounted in New York.

Reed's Quarry 5

This quarry was in the upper part of the formation and produced *Diplodocus*, *Camptosaurus*, *Camarasaurus*, and a theropod in addition to the type specimens of the ornithopod *Dryosaurus altus* (YPM 1876) and the pterosaur *Dermodactylus montanus* (YPM 2020). The quarry is in a medium to coarse-grained sandstone.

Reed's Quarry 7

Also known as the Three Trees Quarry, this locality from a mudstone unit in the upper middle part of the formation produced an adult and juvenile *Goniopholis* and a *Dryosaurus* skeleton (YPM 1882).

Reed's Quarry 12

This locality in the western part of Como Bluff was mainly worked by Arthur Lakes and was in the upper middle part of the formation. The quarry was in a gray silty claystone bed and produced the skeleton of *Stegosaurus ungulatus* that is mounted in the Peabody Museum at Yale (YPM 1853), as well as several other fairly common dinosaur genera and turtle, crocodilian, fish, sphenodontian, and choristodere material.

Little Houston Quarry

This quarry is west of Sundance and has produced the most diverse assemblage of vertebrates from the Morrison in the Black Hills area (Foster and Martin, 1994, 1996; Foster, 2001). The fauna includes several individuals of *Camarasaurus* and *Allosaurus*, along with a number of types of mammals and other microvertebrates. The deposit is in the lower middle part of the formation and represents an accumulation in an abandoned channel (Foster, 1993; Foster and Martin, 1994; Pagnac and DiBenedetto, 1998). The taphonomic characteristics of the accumulation match those of channel-fill deposits outlined by Behrensmeyer (1988). The taxa present include many of the common dinosaur genera, as well as several microvertebrates including four types of mammals (Foster and Martin, 1995, 1996; Martin and Foster, 1998). Vertebrates are preserved in three levels within the quarry: 1) a basal channel sandstone unit; 2) the main level in an interbedded green claystone and laminated siltstone unit; and 3) an overlying claystone unit. The sandstone probably represents the channel in an active stage; the main level would be during a gradual abandonment stage; and the upper deposit, which occurs in claystone above the level of at least one root cast and is lateral to the main part of the quarry, probably represents a stage after infilling of the channel.

Mile 175

This is another locality west of Sundance, Wyoming, which appears to be very close to the top of the formation. Elements here have been collected through surface collection and screen-washing. Taxa preserved include abundant fish, theropods, crocodilians, turtles, the ornithopod ?*Othnielia*, the lungfish *Ceratodus*, and several mammals.

Buffalo Quarry

This site is near Buffalo, Wyoming, and was worked by the Western Paleontological Laboratories. It produced the type skeleton of the new stegosaur *Hesperosaurus* (Carpenter et al., 2001).

Poison Creek Quarry

This locality is southwest of Buffalo and was worked mainly in the 1980s by Bruce Erickson and crews from the Science Museum of Minnesota. The site is in a silty claystone relatively low in the formation and has produced a number of taxa including juveniles of some as well as the rare sauropod *Haplocanthosaurus* and a relatively large *Camptosaurus* (Erickson, 1988). A particularly long theropod metatarsal from this site may belong to *Elaphrosaurus*.

Red Fork Powder River Quarry A

This quarry along the southeast edge of the Bighorn Mountains was worked by Utterback for the Carnegie Museum (McIntosh, 1981). The site is in an overbank pond paleoenvironment (Dodson et al., 1980), and it produced the type specimen of the unique diplodocid sauropod "*Diplodocus*" *hayi* (Holland, 1924). The stratigraphic position of the quarry has not yet been determined.

Red Fork Powder River Quarry B

This quarry is nearby and produced a larger number of dinosaur specimens, including *Diplodocus*, several *Camarasaurus*, *Apatosaurus*, *Allosaurus*, and possibly *Haplocanthosaurus* (McIntosh, 1981).

Sheridan College Quarry 1

This locality is just a meter or so above a sandstone and is near the Poison Creek Quarry. The quarry is also just below a thin sandstone layer which may represent a splay deposit, and the site itself is in green-gray claystone and has produced a number of dinosaur genera including *Camarasaurus* and *Apatosaurus*.

Sheridan College *Allosaurus*

This locality produced a partial *Allosaurus* specimen from a sandstone low in the middle part of the formation.

Reed's Alcova Quarry

This site, in the Alcova area, was worked by W. H. Reed and produced the type specimen of *Stegosaurus longispinus*, which was characterized by very long tail spikes (Gilmore, 1914; Galton, 1990). All that can now be found of the specimen (UW 20503) is the femur, which is similar to that of *S. stenops*.

KU Quarry

This site in the northwestern Black Hills in northeastern Wyoming was originally found just before World War II but was abandoned for more than 50 years. In 1997, crews from the University of Kansas reexcavated the site and found a nearly complete, articulated, and fairly large *Camarasaurus*, along with four nearly complete turtle shells.

SYSTEMATIC PALEONTOLOGY

The following sections review the named taxa currently known from the Morrison Formation. Some taxa that are considered synonymous, or that are of doubtful validity, are still discussed in their own section. Most named species are considered for completeness and for historical review, although the analysis section of this study was done at the generic level. Mammalian species were considered under generic headings due to the number and similarity of named species for many of the taxa.

This is not intended to be a complete revision of the systematics of Morrison Formation vertebrate taxa, and no changes are proposed. It is only meant to outline taxa considered in this analysis. The Morrison taxa are also listed in Table 5.

OSTEICHTHYES

Actinopterygii

Amiiformes indet.

The amiid fish *Ophiopsis* is well-known from the Jurassic of Europe (Bartram, 1975; Patterson, 1982), and was preliminarily identified by Colin Patterson in the Morrison Formation in North America (Prothero, 1981). The American Museum of Natural History found remains of amiids in Quarry 9 and at a new locality called Chuck's Prospect during their expeditions to Como Bluff in the late 1960s. In addition, indeterminate remains of amiids have recently been found in other quarries, but most of the material of amiids from the Morrison Formation appears to be different from *Ophiopsis* (Kirkland, 1998).

Paleonisciformes

Morrolepis schaefferi

This new species has been identified by Jim Kirkland from a quarry high in the Morrison in western Colorado (Kirkland, 1998). Two individuals are known from this site from a nearly complete skeleton and from a caudal fin; several cranial elements of this species have also been identified from southeastern Utah.

Halecostomi

Hulettia hawesi

This is another new fish species that is known from several specimens from two sites in western Colorado (Kirkland, 1998).

Leptolepididae

cf. *Leptolepis* sp.

This genus is known from a single incomplete but articulated skeleton from the Mygatt-Moore Quarry in western Colorado (Kirkland, 1998). The specimen was originally about 12 cm long.

Pycnodontoidea indet.

This group is known from a single tooth from Dinosaur National Monument (Kirkland, 1998).

Dipnoi

Ceratodus guentheri

This lungfish species was identified by Marsh (1878a) and is known from several quarries in the Morrison Formation. Kirkland (1987) listed several specimens of the species from the Marsh-Felch Quarry at Garden Park, though in this paper they were identified as a new species, *C. felchi*. This was an error, as the Garden Park specimens were indeed *C. guentheri*, and the new species, *C. fossanovum*, comprises specimens from Como Bluff (Kirkland, 1998).

Ceratodus fossanovum

This is a new species identified from Quarry 9 and Breakfast Bench at Como Bluff by Kirkland (1987, 1998) and at Ninemile Hill by Trujillo (1999).

Ceratodus robustus

This species was named by Knight (1898) from somewhere in Albany County, Wyoming. The tooth plates of this species are significantly larger, flatter, and more robust than those in other *Ceratodus* species from the Morrison Formation. Specimens of *C. robustus* are also known from Breakfast Bench at Como Bluff and from the Howe Quarry in northern Wyoming.

Ceratodus sp. cf. *C. frazieri*

Ceratodus frazieri is mostly known from the Lower Cretaceous, but two specimens from Oklahoma and South Dakota are very similar to the holotype and may suggest that the species first appears in the Late Jurassic (Kirkland, 1998).

ANURA

Discoglossidae

Enneabatrachus hechti

This recently named species from Quarry 9 at Como Bluff is based on an ilium (Evans and Milner, 1993). The species *Comobatrachus aenigmatis* (Hecht and Estes, 1960) may be a discoglossid but is based on indeterminate material (Estes and Sanchíz, 1982; Milner, 1994).

Pelobatidae

The presence of an unnamed pelobatid at Quarry 9 was noted by Evans and Milner (1993) on the basis of a single right ilium. This specimen extends the range of the family from the mid-Cretaceous to the Late Jurassic (Milner, 1994).

Pipoidea

Rhadinosteus parvus

Several articulated and partially articulated individuals of this new pipoid species were recently identified from the Rainbow Park microvertebrate site in Dinosaur National Monument (Henrici, 1997, 1998).

Anura indet.

The majority of frog material known from the Morrison Formation is taxonomically indeterminate. Marsh (1887a) named *Eobatrachus agilis* from Quarry 9, and at the time of the review of Moodie (1914) this was the only frog known from the formation. Hecht and Estes (1960) named *Comobatrachus aenigmatis* from the same site; however, both of these genera are *nomina dubia*, according to Evans and Milner (1993), as they are based on elements that are ontogenetically quite variable in modern anurans. Other frog material is known from the Garden Park area in Colorado, the Wolf Creek Quarry in northwestern Colorado, and the Little Houston Quarry in northeastern Wyoming, and there is abundant material from Dinosaur National Monument in Utah.

CAUDATA

Caudata indet.

The salamander *Comonecturoides marshi* was named by Hecht and Estes (1960) on the basis of a femur from Quarry 9, but this species is a *nomen dubium*, as the femur is not a distinctive element (Evans and Milner, 1993). According to Evans and Milner (1993), there are two distinct, unnamed types of salamander vertebrae at Quarry 9. Other sites with caudate material include the Wolf Creek Quarry and Ninemile Hill, and the most complete salamander material occurs in the form of two skeletons from Dinosaur National Monument.

REPTILIA

Chelonia

Glyptops plicatulus

This is probably the most common turtle known from the Morrison Formation. Named by Marsh (1890b), its type species is *Compsemys plicatulus* (Cope, 1877a) from high in the Morrison Formation at Garden Park. A nearly complete skeleton was found at Bone Cabin Quarry in Wyoming (Hay, 1908; Gaffney, 1979), but the species is apparently quite widespread and relatively common, as it occurs as fragmentary remains at many quarries. This species is a baenid cryptodiran (Hay, 1908; Gaffney, 1979, 1984) and includes the synonyms *G. utahensis* (Gilmore, 1916) and *G. ornatus* (Marsh, 1890b).

Dinochelys whitei

This more recently named turtle differs from *Glyptops* in having a relatively smooth shell surface (Gaffney, 1979). The type specimen is from Dinosaur National Monument, but the species has since been identified from other quarries, including several Garden Park sites, the Wolf Creek Quarry, the Little Houston Quarry, the Dry Mesa Quarry, and Quarry 9 at Como Bluff.

Uluops uluops

This species occurs high in the Morrison at Breakfast Bench, Como Bluff (Bakker et al., 1990). The skull has a distinct morphology from other Morrison turtles, but the shell sculpture is similar to that of *Glyptops* (Bakker, pers. comm., 1992).

Dorsetochelys buzzops

Bakker (1998) named this new species from the Breakfast Bench region at Como Bluff. It was found high in the formation and is based on a partial skull. Like *Uluops*, the shell texture is similar to that of *Glyptops*.

Sphenodontia

Opisthias rarus

This sphenodontian species was named from Quarry 9 by Gilmore (1910) but has since been identified from numerous quarries and is the most common sphenodontian from the formation. *Opisthias* is also known from the Purbeck Formation (Evans, 1992).

TABLE 5. List of Morrison Formation vertebrate taxa and ecological characterizations for each, with approximate specimen counts.

Taxon	Locomotion/Habitat	Feeding Mode	Estimated Mass (kg)	Count
Hulettia	Aquatic	Invert/Carnivore	<1	5
Morrolepis	Aquatic	Invert/Carnivore	<1	3
Amiiformes	Aquatic	Carnivore	1.1	260
Pycnodontoidea	Aquatic	Invertivore	<1	1
cf. *Leptolepis*	Aquatic	Invert/Carnivore	<1	1
Ceratodus	Aquatic	Invert/Carnivore	3	51
C. robustus	Aquatic	Invert/Carnivore	24	3
Enneabatrachus	Semi-aquatic	Invertivore	<1	3
Rhadinosteus	Semi-aquatic	Invertivore	<1	10
Pelobatidae	Semi-aquatic	Invertivore	<1	1
Anura indet.	Semi-aquatic	Invertivore	<1	11
Caudata	Semi-aquatic	Invertivore	<1	8
Glyptops	Semi-aquatic	Omnivore	5	265
Dinochelys	Semi-aquatic	Omnivore	5	117
Uluops	Semi-aquatic	Omnivore	5	2
Dorsetochelys	Semi-aquatic	Omnivore	5	1
Chelonia indet.	Semi-aquatic	Omnivore	5	249
Opisthias	Specialized Terrestrial	Invertivore	<1	112
Theretairus	Specialized Terrestrial	Invertivore	<1	2
Eilenodon	Specialized Terrestrial	Low Browser	<1	4
Sphenodontia indet.	Specialized Terrestrial	Invertivore	<1	13
Dorsetisaurus	Specialized Terrestrial	Invertivore	<1	5
Parviraptor	Specialized Terrestrial	Invertivore	<1	6
Paramacellodus	Specialized Terrestrial	Invertivore	<1	15
Saurillodon	Specialized Terrestrial	Invertivore	<1	2
Schilleria	Specialized Terrestrial	Invertivore	<1	1
Squamata indet.	Specialized Terrestrial	Invertivore	<1	70
Boidae?	Specialized Terrestrial	Small Carnivore	<1	2
Cteniogenys	Semi-aquatic	Invert/Carnivore	<1	57
Hallopus	Terrestrial	Small Carnivore	5	1
"Fruitachampsa"	Terrestrial	Small Carnivore	5	20
Goniopholis	Semi-aquatic	Medium Carnivore	55	68
Eutretauranosuchus	Semi-aquatic	Medium Carnivore	55	4
Macelognathus	Semi-aquatic	Medium Carnivore	55	1
Mesadactylus	Aerial	Small Carnivore	3.3	3
Dermodactylus	Aerial	Small Carnivore	3.3	1
Kepodactylus	Aerial	Small Carnivore	6.0	1
Comodactylus	Aerial	Small Carnivore	1.4	1
Pterosaur indet.	Aerial	Small Carnivore	3.3	12
Ceratosaurus	Terrestrial	Large Carnivore	524	10
Allosaurus	Terrestrial	Large Carnivore	1010	134
Saurophaganax	Terrestrial	Large Carnivore	2720	2
Torvosaurus	Terrestrial	Large Carnivore	1950	9
Edmarka	Terrestrial	Large Carnivore	1950	2
Marshosaurus	Terrestrial	Medium Carnivore	250	6
Stokesosaurus	Terrestrial	Medium Carnivore	85	3
Ornitholestes	Terrestrial	Small Carnivore	13	2
Coelurus	Terrestrial	Small Carnivore	20	12
Koparion	Terrestrial	Small Carnivore	13	1
Elaphrosaurus	Terrestrial	Medium Carnivore	210	3
Theropoda indet.	Terrestrial	Large Carnivore	1000	35
Brachiosaurus	Terrestrial	High Browser	43,896	12
Camarasaurus	Terrestrial	High Browser	14,000	171

Theretairus antiquus

Named from a single dentary from Quarry 9 at Como Bluff by Simpson (1926b), this sphenodontian has been considered a juvenile of *Opisthias* and thus a junior synonym (Hoffstetter, 1953), though Evans (1992) did not feel that this synonymy was yet solidly established, so the validity of the species is maintained here.

Eilenodon robustus

This sphenodontian is larger than the other genera and has more blunt, transversely expanded teeth. It is thus believed to have been herbivorous. The type specimen was described from the Fruita Paleontological Area in western Colorado (Rasmussen and Callison, 1981a).

Squamata

Parviraptor gilmorei

This anguimorph species was recently described from the Fruita Paleontological Area by Evans (1996). The genus also occurs in the Middle and Upper Jurassic and Lower Cretaceous of England and the Upper Jurassic of Portugal (Evans, 1994).

TABLE 5. (Continued)

Taxon	Locomotion/Habitat	Feeding Mode	Estimated Mass (kg)	Count
C. supremus	Terrestrial	High Browser	47,000	8
Diplodocus	Terrestrial	Medium Browser	12,657	98
"D". hayi	Terrestrial	Medium Browser	12,000	1
Barosaurus	Terrestrial	Medium Browser	11,957	13
Apatosaurus	Terrestrial	Medium Browser	24,247	112
Supersaurus	Terrestrial	High Browser	40,200	2
Seismosaurus	Terrestrial	High Browser	42,500	1
Diplodocidae indet.	Terrestrial	Medium Browser	12,000	21
Haplocanthosaurus	Terrestrial	Medium Browser	7000	11
H. delfsi	Terrestrial	Medium Browser	17,200	1
Dystrophaeus	Terrestrial	Medium Browser	12,000	1
Stegosaurus	Terrestrial	Low Browser	5284	119
Hesperosaurus	Terrestrial	Low Browser	5000	1
Mymoorapelta	Terrestrial	Low Browser	1000	3
Gargoyleosaurus	Terrestrial	Low Browser	1000	1
Ankylosauria indet.	Terrestrial	Low Browser	1000	4
cf. *Echinodon*	Terrestrial	Low Browser	5	4
Othnielia	Terrestrial	Low Browser	5	22
Drinker	Terrestrial	Low Browser	5	12
Dryosaurus	Terrestrial	Low Browser	114	29
Camptosaurus	Terrestrial	Low Browser	830	59
Ornithopoda indet.	Terrestrial	Low Broswer	~450	10
Docodon	Specialized Terrestrial	Omnivore	<1	84
Ctenacodon	Specialized Terrestrial	Omnivore	<1	29
Psalodon	Specialized Terrestrial	Omnivore	<1	20
Glirodon	Specialized Terrestrial	Omnivore	<1	2
Zofiabaatar	Specialized Terrestrial	Omnivore	<1	1
Multituberculata indet.	Specialized Terrestrial	Omnivore	<1	16
Triconolestes	Specialized Terrestrial	Invert/Carnivore	<1	1
Aploconodon	Specialized Terrestrial	Invert/Carnivore	<1	1
Phascolotheridium	Specialized Terrestrial	Invert/Carnivore	<1	1
Priacodon	Specialized Terrestrial	Invert/Carnivore	<1	25
Trioracodon	Specialized Terrestrial	Invert/Carnivore	<1	13
Triconodonta indet.	Specialized Terrestrial	Invert/Carnivore	<1	7
Amphidon	Specialized Terrestrial	Invertivore	<1	2
Tinodon	Specialized Terrestrial	Invertivore	<1	15
Symmetrodonta indet.	Specialized Terrestrial	Invertivore	<1	3
Araeodon	Specialized Terrestrial	Invertivore	<1	1
Archaeotrigon	Specialized Terrestrial	Invertivore	<1	9
Euthlastus	Specialized Terrestrial	Invertivore	<1	3
Foxraptor	Specialized Terrestrial	Invertivore	<1	1
Paurodon	Specialized Terrestrial	Invertivore	<1	2
Comotherium	Specialized Terrestrial	Invertivore	<1	2
Pelicopsis	Specialized Terrestrial	Invertivore	<1	1
Tathiodon	Specialized Terrestrial	Invertivore	<1	1
Paurodontidae indet.	Specialized Terrestrial	Invertivore	<1	6
Amblotherium	Specialized Terrestrial	Invertivore	<1	37
Dryolestes	Specialized Terrestrial	Invertivore	<1	60
Kepolestes	Specialized Terrestrial	Invertivore	<1	1
Laolestes	Specialized Terrestrial	Invertivore	<1	40
Melanodon	Specialized Terrestrial	Invertivore	<1	13
Miccylotyrans	Specialized Terrestrial	Invertivore	<1	1
Dryolestidae indet.	Specialized Terrestrial	Invertivore	<1	20
Mammalia indet.	Specialized Terrestrial	Invertivore	<1	126

Dorsetisaurus sp.

The anguimorph *Dorsetisaurus* was described by Hoffstetter (1967) from the Upper Jurassic of England and identified by Prothero and Estes (1980) in the American Museum collections from Quarry 9 at Como Bluff. It has been found since at several other Morrison sites. The genus also occurs in the Upper Jurassic of Portugal (Seiffert, 1973; Evans, 1994).

Saurillodon sp.

Saurillodon is a scincomorph lizard known from the Middle Jurassic of England and Scotland and the Upper Jurassic of Portugal and recently identified in the Morrison Formation from the Fruita Paleontological Area in western Colorado (Evans and Milner, 1994; Evans, 1996).

Paramacellodus sp.

Paramacellodus is another scincomorph. The type species, *P. oweni*, was named by Hoffstetter (1967), and the genus was identified in the Morrison Formation collections from Quarry 9 at Como Bluff by Prothero and Estes (1980). This genus is also known

from the Middle Jurassic of Scotland and the Lower Cretaceous of England, Spain, and Morocco and spans nearly 60 ma (Evans and Chure, 1998). It is present in the Morrison Formation at Fruita and the Rainbow Park localities in Dinosaur National Monument (Evans, 1996). It has recently been reported from the Guimarota locality in the Upper Jurassic of Portugal (Broschinski, 2000).

Schilleria utahensis

Evans and Chure (1999) named this new lizard species based on a specimen from Dinosaur National Monument. The familial assignment for the taxon is still undetermined.

Serpentes

Boidae?

The Morrison Formation in the Fruita Paleontological Area in western Colorado has produced a jaw that appears to represent a Jurassic snake, currently the oldest known (Callison, 1987; Kirkland, pers. comm., 1997). No other elements of the animal have been identified, so little is known of this important taxon.

Choristodera

Cteniogenys antiquus

This species was described by Gilmore (1928) on the basis of several jaw fragments from Quarry 9. Gilmore tentatively identified the animal as a lizard but noted that this was not certain and mentioned that it could also be a frog. New material from Europe has demonstrated that *Cteniogenys* is neither, but is rather an archosauromorph and an early member of the Choristodera (Evans, 1989, 1990, 1991). The genus is also known from the Middle Jurassic of England and the Late Jurassic of Portugal.

Crocodylia

Hallopus victor

Marsh (1877a) briefly described and named a specimen from an unknown level at Garden Park, in Fremont County, Colorado, as *Nanosaurus victor*. Marsh (1881a) later renamed the specimen *Hallopus victor* and identified it as a small dinosaur. Walker (1970) redescribed the specimen and identified it as a small, cursorial terrestrial crocodilian, and Ague et al. (1995) demonstrated that, despite speculation that the specimen had come from Triassic beds, it had in fact been collected from high in the Morrison Formation near Cope's quarries at the Nipple. Carroll (1988) included this genus in its own suborder of the Crocodylia.

"Fruitachampsa callisoni"

Other cursorial mesosuchian crocodiles occur in the Morrison Formation as well. The first was described as *"Fruitachampsa callisoni"* by Clark (1985) and occurred in the lower Brushy Basin Member at the Fruita Paleontological Area in western Colorado. *"Fruitachampsa"* is a housecat-sized animal with long limbs and a relatively short skull. Chure et al. (1991) briefly described another, unnamed form from a nesting locality in the Salt Wash Member near Delta, also in western Colorado (Hirsch et al., 1987; Young 1991). Kirkland (1994) reported fragments of an unidentified cursorial crocodilian from another eggshell site at Fruita also.

Hoplosuchus kayi

This small crocodilian species was described by Gilmore (1926), and the nearly complete, articulated skeleton is just 15 cm long. The specimen (CM 11361) was found at Dinosaur National Monument, stratigraphically below the Carnegie Museum quarry and was identified by Romer (1956) as an atoposaurid crocodilian. The limbs are fairly slender, and the skull is relatively large, so the possibility remains that this is a juvenile of a known terrestrial or, less likely, semi-aquatic crocodilian. Clark (1986) noted that *Hoplosuchus*, though articulated, is not well-preserved enough to be certain of its validity but stated that the structure of the squamosal may be unique.

Macelognathus vagans

This species is based on the symphyseal and anterior portions of the dentaries of a single specimen (YPM 1415) and is from Quarry 9 at Como Bluff (Marsh, 1884b). Ostrom (1971) identified the specimen as likely that of an unknown, relatively large crocodilian. The symphysis and anterior dentaries are fairly flat and the anterior portion of the symphysis is edentulous, which separate this species from other known Morrison crocodilians. Interestingly, Ostrom (1971) also noted that *Macelognathus* shared some features in common with the Choristodera, although this group was at the time unknown in the Morrison Formation. However, there are significant differences in form and size between *Macelognathus* and *Cteniogenys*, now known to be a choristoderan.

Goniopholis

G. felix, G. lucasii, G. gilmorei, G. stovalli

Four species of the relatively large, semi-aquatic crocodilian genus *Goniopholis* have been named from the Morrison Formation (Steel, 1973). The genus was named by Owen from deposits in England and more extensively illustrated several years later (Owen, 1878). Marsh described the relatively small species *G. felix* (originally as *Diplosaurus*) from the Yale quarries at Morrison, Colorado; Cope described *G. lucasii* (originally as *Amphicotylus*), from the Garden Park area in Colorado, and Mook (1933, 1942) described a second specimen from the same locality and provisionally referred a small crocodilian specimen from the Marsh-Felch Quarry at Garden Park to this species; Holland (1905) described *G. gilmorei* from Wyoming; and Mook (1964) described *G. stovalli* from the quarries in Cimarron County, Oklahoma.

The validities of these species are difficult to assess. All are known from skull material, but the morphological differences between them are subtle and, as most other goniopholid material from the formation is fragmentary, most species are known from a single specimen. It may be that most specimens of *Goniopholis* could be referred to *G. felix*.

Eutretauranosuchus delfsi

Eutretauranosuchus was described by Mook (1967) from a specimen collected by the Cleveland Museum of Natural History from low in the Morrison Formation at Garden Park, Colorado. The specimen (CMNH 8028) is moderately small (skull length ~218 mm), and the skull is quite distinct from any species of *Goniopholis*, and modern classifications of the crocodilians do not view *Eutretauranosuchus* and *Goniopholis* as forming a monophyletic "Goniopholididae" (Clark, 1994). *Eutretauranosuchus* is in fact most closely related to dyrosaurids and *Pholidosaurus*, among others, and is part of a larger clade including *Bernissartia* and eusuchians, in addition to *Goniopholis* (Clark, 1994). *Eutretauranosuchus* also has been identified from several other sites in the Morrison.

Pterosauria

Rhamphorhynchoidea

Comodactylus ostromi

This species was named by Galton (1981), based on a metacarpal from Quarry 9 at Como Bluff. The animal seems to have been one of the larger Morrison pterosaurs, as Wellnhofer (1991) estimated the wing span as approximately 2.5 meters.

Pterodactyloidea

Dermodactylus montanus

Marsh (1878b) described *Dermodactylus* based on a metac-

arpal fragment from Quarry 5 at Como Bluff, and this was the first evidence of Jurassic pterosaurs in North America. The specimen represents a somewhat smaller animal with a wing span of approximately 1 meter (Wellnhofer, 1991).

Mesadactylus ornithosphyos

This species is known from numerous disarticulated remains from the Dry Mesa Quarry in western Colorado (Jensen and Ostrom, 1977; Jensen and Padian, 1989). The synsacrum of this species consists of uniquely fused vertebrae, and the animal seems to have been smaller than other Morrison pterodactyloids (Wellnhofer, 1991; Smith et al., 2002).

Kepodactylus insperatus

This species of pterodacyloid was named from a humerus and several other elements from the Small Quarry at Garden Park, Colorado (Harris and Carpenter, 1996). It is significantly larger than other pterosaur specimens known from the Morrison Formation.

Pterosauria indet.

Marsh (1881b) described *Laopteryx priscus*, a small, fragmentary skull from Quarry 9, as that of a Jurassic bird. Ostrom (1986) determined that there was no more reason to identify this specimen as a bird than as a pterosaur and that the latter identification was far more likely. Fragmentary and indeterminate pterosaur material is also known from several other quarries but is generally rare in the Morrison.

Dinosauria

Saurischia

Theropoda

Ceratosauria

Ceratosaurus nasicornis

Ceratosaurus was named by Marsh (1884a) on the basis of a partial skeleton (USNM 4735) from the Marsh-Felch Quarry at Garden Park, Colorado, and was described in detail by Gilmore (1920). Several partial skeletons of other specimens have been found elsewhere since, and Rowe and Gauthier (1990) listed this species within the primitive theropod group Ceratosauria. *Ceratosaurus magnicornis* (MWC 1) and *C. dentisulcatus* (UUVP 674) were recently named by Madsen and Welles (2000).

Tetanurae

Megalosauridae

Torvosaurus tanneri

Named by Galton and Jensen (1979) from the Dry Mesa Quarry in western Colorado, this species of megalosaur has been described in detail by Britt (1991). *Torvosaurus* was relatively large and robust and was the first megalosaurid found in the Morrison. This species has been referred to Carnosauria *incertae sedis* by Molnar et al. (1990) and joined with the Spinosauridae in the Spinosauroidea by Sereno (1999). It also has been classified as the sister taxon to *Megalosaurus* + all other tetanurans by Holtz (1994). Thus, the validity of the Megalosauridae as a natural group still has not been established.

Edmarka rex

This megalosaurid species was described by Bakker et al. (1992), based on several elements from the Nail Quarry in the eastern Como Bluff region. The specimen is a large, robust megalosaurid with subtle differences from *Torvosaurus*, and *Edmarka* may in fact be an individual variant of the referred material of *Torvosaurus* from Dry Mesa.

Allosauridae

Allosaurus fragilis

Allosaurus is the most common theropod genus found in the Morrison Formation. *A. fragilis* was briefly described by Marsh (1877b) from Garden Park, Colorado, and has been stated as including *A. lucaris* and the other genera *Antrodemus*, *Labrosaurus*, *Creosaurus*, and *Hypsirophus* as junior synonyms (Molnar et al., 1990). The main osteological description of *Allosaurus fragilis* was done by Madsen (1976a). *Epanterias amplexus*, named from high in the Morrison by Cope (1878b), may be synonymous with *Allosaurus* (Molnar et al., 1990), though Bakker et al. (1992) considered it a distinct species. Paul (1988a) considered *A. atrox* as a species distinct from *A. fragilis*, and Madsen (pers. comm., 1996) agrees that there may be more than one species of *Allosaurus* in this material, though this has not been clearly established. Smith (1996, 1998) saw no evidence for more than one species (*A. fragilis*) among current material.

Allosaurus **n. sp.**

A new specimen from low in the formation at Dinosaur National Monument (DINO 11541) appears to represent a new species of *Allosaurus* (Chure, pers. comm., 1997). This specimen is one of the most complete and best articulated of all known *Allosaurus* specimens and has a number of differences from *A. fragilis*, including an extremely thin coracoid. The specimen will be named by Dan Chure in a future American Museum Bulletin.

Saurophaganax maximus

This species was found high in the Morrison at Stovall's Quarry 1 in Oklahoma and named *Saurophagus* by Ray (1941). Molnar et al. (1990) considered it a synonym of *Allosaurus*, but Chure (1995) has reexamined the material and determined that it is a valid species. Chure (1995) also altered the genus name, as the original name had been claimed to be a *nomen nudum* and preoccupied (Camp et al., 1953), and the lectotype was not distinctive. *Saurophaganax* is a very large allosaurid and has been estimated to have weighed approximately 2.7 tonnes (Chure, 1995).

Epanterias amplexus

Named by Cope (1878a) from high in the Morrison at Garden Park, Colorado, this large species was considered valid by Bakker et al. (1992), and has been identified at another locality in the northern Front Range of Colorado (Bakker et al., 1990), though Chure (1995) noted that *Epanterias* is indistinguishable from *Allosaurus* and *Saurophaganax*. The type cervical neural arch of *Epanterias amplexus* (AMNH 5767) is approximately 20% larger than that of a moderately large *Allosaurus fragilis* (AMNH 666) from Bone Cabin Quarry but is morphologically very similar. The type specimen is likely a large individual of *Allosaurus*.

Coelurosauria

Koparion douglassi

This recently described species is based on a single, very small tooth and is referred to the Troodontidae (Chure, 1994). It is known from the DNM-94 quarry at Rainbow Park in the upper Brushy Basin Member in the northern part of Dinosaur National Monument, Utah. Most members of the Troodontidae are Late Cretaceous, but having troodontids in the Late Jurassic may not be surprising if they are indeed a sister taxon to birds (Currie, 1987). Nearly all troodontids were small, highly cursorial predators with relatively large numbers of teeth for the size of their jaws (Osmólska and Barsbold, 1990).

Ornitholestes hermanni

Ornitholestes was named by Osborn (1903) and based on a

partial skeleton with a skull (AMNH 619) from Bone Cabin Quarry in Wyoming. Also from Bone Cabin is the referred manus of a second individual, which, as Paul (1988b) noted, is a tentative identification because much of the hand is missing from the holotype. *Ornitholestes* was a fairly small, lightly built predator, approximately 2 m long and weighing about 12.6 kg (Paul, 1988a). The skull is relatively one of the lightest built of Morrison theropods and is 14.5 cm long with moderately conical teeth, the longest and straightest of which are in the anterior maxilla-posterior premaxilla region. Norman (1990) listed the species as a problematic "coelurosaur," although Gauthier (1986) and Holtz (1994) more specifically included it within the Maniraptora. More recent analyses, however, have removed it from the Maniraptora but retained it as a coelurosaur (Holtz, 1998; Norell et al., 2001).

Coelurus fragilis

This species was named by Marsh (1879b) from Quarry 13 at Como Bluff and, as Gilmore (1920) and Norman (1990) determined, includes *C. agilis* (Marsh, 1884a) as a junior synonym. Ostrom (1980b) determined that this species was distinct from *Ornitholestes*, as there had been some debate on that point. A relatively small and highly cursorial form, *Coelurus* has been assigned to the Maniraptora by Gauthier (1986), though Norman (1990) noted that a key maniraptoran character (cervical hypapophyses) is lacking and deferred assignment of the species to a particular group until after more work has been done on the type specimen by John Ostrom. A larger and more complete specimen was recently found near Bone Cabin Quarry in Wyoming and suggests that *Coelurus* grew to be larger than prevously recognized and may have been a maniraptoran (Miles et al., 1998).

Problematic Theropoda

Stokesosaurus clevelandi

This species was described by Madsen (1974) from the Cleveland-Lloyd Quarry in Utah, and provisionally referred to the Tyrannosauridae, and later Molnar et al. (1990) listed *Stokesosaurus* as Carnosauria *incertae sedis*. Holtz (pers. comm., 2001) includes it in the Tyrannosauroidea. An ilium of a juvenile *Stokesosaurus* was found in 1980 at a second locality in western South Dakota (Foster and Chure, 2000). The ilium of this species has a distinct vertical ridge rising from the acetabular hood to the dorsal edge of the iliac blade.

Marshosaurus bicentesimus

This species was named by Madsen (1976b) from the Cleveland-Lloyd Quarry in Utah, and was not assigned to a known family. Likewise, Molnar (1990b) has *Marshosaurus* listed as Theropoda *incertae sedis*. A moderate-sized form, *Marshosaurus* is unlike more derived carnosaurs such as allosaurids, but has some similarities to both *Coelurus* and ceratosaurs.

Elaphrosaurus sp.

The species *Elaphrosaurus bambergi* was described by Janensch (1920) from the Late Jurassic Tendaguru deposits of what is now Tanzania. It was traditionally identified as a primitive ornithomimid (Barsbold and Osmólska, 1990), although Holtz (1994) included it within the Ceratosauria, and most all recent work suggests it is an abelisauroid (Chure, pers. comm., 1998). Galton (1982b) first identified a humerus from the Marsh-Felch Quarry at Garden Park, Colorado, as that of *Elaphrosaurus* sp., and a proximal tibia from the nearby Small Quarry has recently been referred to the genus (Chure, 2001).

Sauropoda

Cetiosauridae

Haplocanthosaurus priscus

This species was described by Hatcher (1903) and includes *H. utterbacki* Hatcher according to McIntosh and Williams (1988). A moderate-sized sauropod originally found in the Marsh-Felch Quarry at Garden Park, Colorado, the genus has since been identified from several other quarries in the mid to lower parts of the Morrison. Most of these additional specimens seem to be of the moderate size of this species and may be referable to it. *Haplocanthosaurus* may be more closely related to *Camarasaurus* and *Brachiosaurus* than to the diplodocids, though this association is quite uncertain in most analyses (Upchurch, 1995; Wilson and Sereno, 1998).

Haplocanthosaurus delfsi

This larger species of *Haplocanthosaurus* was collected from Garden Park by Ed Delfs and a crew from the Cleveland Museum of Natural History in the mid 1950s. McIntosh and Williams (1988) recognized its specific distinction from *H. priscus*. It is from the lower Morrison.

Brachiosauridae

Brachiosaurus altithorax

Riggs (1903) named and described the holotype of *Brachiosaurus*, which had been excavated from near Grand Junction in western Colorado. This is a very large sauropod characterized by slender and long forelimbs. It has since been found at several other quarries, including Dry Mesa, Potter Creek, Jensen-Jensen, and Marsh-Felch. Most *Brachiosaurus* specimens in the Morrison Formation are probably referable to this species, as is the brachiosaurid scapula from the Dry Mesa Quarry (BYU 9462) referred to *Ultrasauros macintoshi* by Jensen (1985). The type dorsal of *Ultrasauros macintoshi* (BYU 9044) is not clearly brachiosaurid and may even be diplodocid (Curtice et al., 1996). Paul (1988c) noted that BYU 9462 is no larger than *Brachiosaurus brancai* scapulae from Tendaguru, Tanzania, and that the largest *Brachiosaurus* specimens were from animals that probably weighed about 50 tons.

Camarasauridae

Camarasaurus supremus

Three individuals of this species (AMNH 5760, AMNH 5761, AMNH 5761a) were found by crews working for E. D. Cope high in the Morrison at Garden Park. Cope (1877b) described and named the species, which McIntosh (1990b) noted cannot easily be distinguished from *C. lentus* except by size. Osborn and Mook (1921) further described and illustrated Cope's Garden Park specimens. *C. supremus* is a massive animal with a femur length of 1.8 m (AMNH 5761a) whereas most other adult specimens referable to *Camarasaurus* have femora about 1.2 m long. Other elements of the *C. supremus* skeleton are similarly large. This species includes *C. leptodirus* as well.

Camarasaurus lentus

This species was named by Marsh (1889) and is, along with *C. grandis*, one of the more common sauropod species in the Morrison Formation. It is nearly indistinguishable from *C. supremus*, other than in its smaller size. The species also includes *Camarasaurus annae* (Ellinger, 1950) and *Uintasaurus douglassi* (Holland, 1919), and much of the *Camarasaurus* material at the Dinosaur National Monument Quarry has been referred to *C. lentus* (Madsen et al., 1995).

Camarasaurus grandis

This species, named by Marsh (1877b), is relatively common and is distinguished by the placement of the neural arch

pedicels high above the neural canal in the anterior dorsals (McIntosh, 1990a, b). The species also includes *Morosaurus impar* (Marsh, 1878c) and *Morosaurus robustus* (Marsh, 1878d); it is also similar in size to *C. lentus*. Although the postcrania of *C. grandis* are distinct from *C. supremus* and *C. lentus*, the skull elements are indistinguishable (Madsen et al., 1995).

Camarasaurus lewisi

This species is based on a single specimen from western Colorado described and named by Jensen (1988) as *Cathetosaurus lewisi*. McIntosh et al. (1996) redescribed the specimen (BYU 9047) and recognized it as a new species of *Camarasaurus*. The specimen apparently represents an old individual, and many of its distinguishing characters are age related, but several characters, including narrow clefts in the dorsal neural spines back nearly to the sacrals, are of taxonomic significance (McIntosh et al., 1996).

Diplodocidae

Diplodocus longus

Marsh (1878d) named this species based on a series of caudal vertebrae (YPM 1920) from the Marsh-Felch Quarry at Garden Park, Colorado. Only two of the vertebrae preserved are still in good condition, but this is the species to which most *Diplodocus* specimens have been referred. *D. lacustris*, from Quarry 5 at Morrison, Colorado, may belong to this species, or even the genus *Apatosaurus* (McIntosh, 1990b).

Diplodocus carnegii

This species was described by Hatcher (1901) based on two specimens (CM 84, CM 94) from the Carnegie Museum Quarry D at Sheep Creek, Wyoming. McIntosh (1990a, b) retained *D. carnegii*, in addition to *D. longus*, because *D. carnegii* was based on better material, but noted that Hatcher's characters for distinguishing the two were probably due to individual variation.

"Diplodocus" hayi

Holland (1924) named this species based on a single partial skeleton from Quarry A on the Red Fork of the Powder River on the east edge of the Bighorn Mountains in Wyoming. This species is quite different from all other known specimens of *Diplodocus*, particularly in the more robust limbs and in the caudal vertebrae, and may even represent a separate genus (McIntosh, pers. comm., 1994).

Apatosaurus excelsus

This species is one to which much Morrison *Apatosaurus* material has been referred. It was named by Marsh (1879a) as *Brontosaurus excelsus*, based on YPM 1980, and is distinguished by its moderate size relative to *A. ajax* and by its anterior cervical rib extensions and more slender limbs relative to *A. louisae*. This species includes *Brontosaurus amplus* (Marsh, 1881a) and *Elosaurus parvus* (Peterson and Gilmore, 1902), the latter a very young individual. Other than by size, *A. excelsus* is not particularly distinguishable from *A. ajax*, but is probably distinct from *A. louisae*.

Apatosaurus louisae

This species, based on CM 3018 from the Dinosaur National Monument quarry, was named by Holland (1915) and described in detail by Gilmore (1936). The cervical ribs lack the anterior extensions of other species, and the limbs of *A. louisae* are some of the more robust among any Morrison sauropods.

Apatosaurus ajax

Several individuals of this species were among the first forms described from the Morrison (Marsh, 1877b). A large species that includes *A. laticollis* and *Atlantosaurus immanis*, *A. ajax* is nearly indistinguishable from *A. excelsus*, except by size. Interestingly, although *A. ajax* is generally larger than *A. excelsus*, at least one individual of *A. ajax* does not appear to be fully adult (McIntosh, 1990b).

Apatosaurus yahnahpin

Found low in the Morrison in the eastern part of Como Bluff, *A. yahnahpin* is characterized by a scapula with a relatively expanded distal end and may represent an early form of the genus (Filla and Redman, 1994). The specimen was found semi-articulated in overbank deposits. Bakker (1998) renamed this specimen *Eobrontosaurus yahnahpin*.

Barosaurus lentus

Marsh (1890a) named *Barosaurus* on the basis of YPM 429, which was found north of Rapid City, South Dakota, in 1889. The type specimen was described in more detail by Lull (1919). This species is very similar to *Diplodocus*, and in many elements the two are indistinguishable, but the cervical vertebrae of *Barosaurus* are particularly elongate, more so than in *Diplodocus*. Additional partial skeletons of *B. lentus* have been found at the Dinosaur National Monument quarry in Utah, the Howe Quarry in Wyoming, and at the Wonderland Quarry several kilometers south of the type locality in South Dakota (McIntosh, 1981; Brown, 1935; Foster, 1996a). A second species named by Marsh (1890a) as *B. affinis* from the type locality is an indeterminate, smaller diplodocid. Two additional species, *B. africanus* (Fraas, 1908) and *B. gracilis* (Janensch, 1961), have been reported from the Tendaguru deposits in Tanzania.

Amphicoelias altus

This species is based on two dorsals, a femur, and a referred ulna from high in the Morrison at Cope's Garden Park quarries (Cope, 1877d). Wilson and Smith (1996) refer material from Montana to this genus based on the structure of the femur, but as the type femur and dorsals are large but otherwise indistinguishable from one morphotype of *Diplodocus* (characterized by AMNH 223 and USNM 10865), this referral is questionable (Curtice et al., 1997). It is possible the Montana material represents a new form. *Amphicoelias fragillimus* (Cope, 1878b) is based on a single dorsal neural spine that is now lost but was reported to be quite large. If it was similar in proportion to *Diplodocus*, as seems likely, Jack McIntosh has estimated the femur of the animal as having been approximately 3 meters in length. The genus *Amphicoelias* is here considered a junior synonym of *Diplodocus*, as the type material cannot be reliably distinguished from that genus.

Supersaurus vivianae

Based on a specimen from the Dry Mesa Quarry (Jensen, 1985), this relatively large sauropod appears to be distinct from other diplodocids, based on caudal morphology (Curtice, 1996), though it is conceivable that it is a very large individual of *Barosaurus* (Curtice, pers. comm., 1996).

Dystrophaeus viaemalae

Dystrophaeus (Cope, 1877c) is the oldest sauropod known from the Morrison; it is from the Tidwell Member in eastern Utah (Gillette, 1996a, 1996b). Not enough of the specimen is yet available to be certain, but, based on the slender forelimb material, it may be close to the Diplodocidae. Some cetiosaurids, however, have similarly slender forelimb elements.

Dyslocosaurus polyonychius

This form is based on a lower hind limb and pes from the Lance Creek area of eastern Wyoming (McIntosh et al., 1992). It is unusual in having unguals on all five digits of the pes, but is oth-

erwise diplodocid. Unfortunately, though the preservation seems similar to Morrison specimens, it is not absolutely certain that it came from one of the small Morrison outcrops in the area and could possibly be Cretaceous. Therefore, it will not be included in this analysis.

Seismosaurus hallorum

This species from northwestern New Mexico was named by Gillette (1991) based on a partial articulated skeleton from a channel sandstone unit. It is, like *Supersaurus*, a very large diplodocid, but it has not yet been clearly distinguished from *Diplodocus* (McIntosh, 1997). Lucas and Heckert (2000) even refer to the specimen as *D. hallorum*, although a formal comparison synonymizing *Seismosaurus* with *Diplodocus* has not been done.

Dystylosaurus edwini

Jensen (1985) described this species based on a single dorsal from the Dry Mesa Quarry. Its familial identification has been uncertain, some referring it to the Brachiosauridae, some to the Diplodocidae, and some to family indet. Curtice (pers. comm., 2001) believes the holotype is actually part of the associated skeleton of *Supersaurus*.

Ornithischia

Thyreophora

Stegosauria

Hesperosaurus mjosi

Carpenter and Miles (1997) first reported, but did not name, this new genus and species of primitive stegosaur from the Morrison Formation at the Buffalo Quarry in north-central Wyoming. The specimen has a more primitive skull than *Stegosaurus*, oval dermal plates, and low-arched dorsal vertebrae (Carpenter et al., 2001).

Stegosaurus ungulatus

This species is based on good material from Quarry 12 at Como Bluff (Marsh 1879c). Initially, Galton (1990) included this species in *S. armatus*, but too little of that specimen has been prepared to be certain (Carpenter and Galton, 2001). *Stegosaurus ungulatus* is characterized by elongate radii, ulnae, and femora, but does not have four pairs of tail spikes (Carpenter and Galton, 2001) as had been previously believed.

Stegosaurus armatus

Marsh (1877c) named this species based on material collected by Arthur Lakes from Morrison, Colorado. It includes *S. sulcatus* (Marsh, 1887b), *S. duplex* (Marsh, 1887b), and *Hypsirhophus seeleyanus* (Cope, 1879), according to Galton (1990).

Stegosaurus stenops

Marsh (1887b) named this species, which includes *Diracodon laticeps* (Marsh, 1881a). It is known from numerous specimens and is distinguished by having ventrally keeled sacral vertebrae and an unelongated femur.

Stegosaurus longispinus

This species was named by Gilmore (1914) and was collected by W.H. Reed near Alcova, Wyoming. Unfortunately, the femur is about all that can be found of the specimen (UW 20503) now, but the species is characterized by particularly long tail spikes. The femur is similar in form to *S. stenops*.

Ankylosauria

Mymoorapelta maysi

Carpenter and Kirkland (1994) named this species, the first ankylosaur described from the Morrison, from disarticulated material representing at least two individuals at the Mygatt-Moore Quarry in western Colorado. Another specimen (MWC 2610) has been found at Cactus Park in the Uncompahgre Plateau region.

Gargoyleosaurus parkpini

This new genus and species from the new excavations at Bone Cabin Quarry was described by Carpenter et al. (1998) as being close to Cretaceous anykylosaurs. The specimen consists of a partial skeleton with a well-preserved skull.

Ornithopoda

Heterodontosauridae?

cf. *Echinodon*

A small jaw from the Fruita Paleontological Area (LACM 128258), which is similar to that of *Echinodon*, contains typical primitive ornithopod teeth and a single caniniform tooth near the front of the jaw as in heterodontosaurids (pers. obs.; Galton, 2002). Approximately four individuals are represented at the Fruita locality, as several other cranial and postcranial elements have been referred to this taxon, which is close to *Echinodon* but probably represents a new genus (Galton, pers. comm., 2002).

Hypsilophodontidae

Othnielia rex

Galton (1977) named this species based on Marsh's (1877b) naming of *Nanosaurus rex*. *Laosaurus gracilis* (Marsh, 1878d) and *L. consors* (Marsh, 1894) are synonyms, according to Sues and Norman (1990). This is a small ornithopod with relatively primitive teeth and is known from numerous sites.

Drinker nisti

Bakker et al. (1990) named this small ornithopod on the basis of teeth that are similar to *Othnielia* and that have an accessory ridge of denticles. This accessory ridge is sometimes present in specimens of *Othnielia*, however (R. Scheetz, pers. comm., 1998). Most specimens of *Drinker* have been identified in the Como Bluff region and are slightly smaller than most *Othnielia*.

Dryosauridae

Dryosaurus altus

This species was described by Marsh (1878d) based on *Laosaurus altus*. A second species, *D. lettowvorbecki* (Virchow, 1919), is known from Tanzania. Galton (1983) described the skull as well as addtional material of *D. altus* from the Morrison. This medium-sized ornithopod is somewhat similar to *Othnielia*, although it is generally larger and has more advanced teeth. It is known from a number of localities in the formation.

Camptosauridae

Camptosaurus dispar

Marsh (1879b) named *Camptosaurus dispar*, for which Norman and Weishampel (1990) consider there to be numerous synonyms including *C. medius*, *C. nanus* (Marsh, 1894), and *C. browni* (Gilmore, 1909). *C.? depressus* may not even be from the Morrison (Norman and Weishampel, 1990). The relatively smaller type specimens and referred material of *C. medius* and *C. nanus* contain some unfused vertebral neural arches and probably represent young individuals referable to *C. dispar*. Many individuals of *Camptosaurus* are known from Quarry 13 in the eastern part of Como Bluff.

Other ornithopods

The species *Laosaurus celer* (Marsh, 1878c) and *Nanosaurus agilis* (Marsh, 1877a) are considered *nomina dubia* by Sues and Norman (1990), though Galton (1983) considered *N. agilis* valid.

MAMMALIA

Docodonta

Docodon

Docodon victor was named by Marsh (1880). Other species include *D. striatus* (Marsh, 1881c), *D. affinis* (Marsh, 1887c), *D. crassus* (Marsh, 1887c), and *D. superus* (Simpson, 1929), this last species consisting of upper dentitions. Probably all of this material is referable to *D. victor*, as Jenkins (1969) concluded that *Docodon* may be monospecific, though he did not conduct any formal synonymization. *Docodon* is one of the more common and widespread mammal genera in the Morrison Formation, occurring at several sites around Como Bluff and at Garden Park, as well as at the Little Houston Quarry in northeastern Wyoming. Interestingly, it is unknown or very rare at Fruita and Rainbow Park.

Multituberculata

Ctenacodon

O. C. Marsh named two species of *Ctenacodon*, *C. serratus* (Marsh, 1879d) and *C. laticeps* (Marsh, 1881c), from Quarry 9. Simpson (1929) named *C. scindens*. *Ctenacodon* is a relatively small multituberculate from the Morrison and, like the other multituberculate forms in the formation, has several blade-like premolars increasing in size posteriorly.

Psalodon

Psalodon was recognized as a separate form and named by Simpson (1926c) based on upper jaw material described by Marsh (1887c) as *Ctenacodon potens* (*P. potens*) and *Allodon fortis* (*P. fortis*). Simpson (1929) also named ?*Psalodon marshi* for lower jaw elements probably attributable to this genus. *Psalodon* is very similar to *Ctenacodon* but is noticeably larger. The type material comes from Quarry 9 and a lower jaw probably belonging to *Psalodon* is known from the Little Houston Quarry (Martin and Foster, 1998). Simmons (1993) noted that *Psalodon* and *Ctenacodon* form a monophyletic Allodontidae.

Zofiabaatar

Bakker et al. (1990) named and described a new multituberculate from the Breakfast Bench locality in the eastern part of Como Bluff. This species, *Zofiabaatar pulcher*, is based on a relatively robust lower jaw that is more similar to some Lower Cretaceous forms than other Morrison multituberculates and is from relatively high in the formation. Carpenter (1998b) redescribed the specimen.

Glirodon

Engelmann et al. (1990) and Bradley et al. (1997) mentioned a new multituberculate from Fruita and Rainbow Park that has recently been named and described as *Glirodon grandis* (Engelmann and Callison, 1999). This multituberculate seems to form a monophyletic group with *Bolodon* and two taxa which were previously considered primitive taeniolabidoids, *Eobaatar* and *Monobaatar* (Simmons, 1993).

Triconodonta

Priacodon

Marsh (1879d) named *P. robustus*, based on a lower jaw, and *P. ferox* (Marsh, 1880) from upper and lower dentitions. Both species are from Quarry 9 at Como Bluff. Simpson (1925b) named the species *P. gradaevus* and *P. lulli* from upper dentions from Quarry 9, and Rasmussen and Callison (1981b) described *P. fruitaensis* from a lower jaw at the Fruita Paleontological Area in Colorado. Thus, if all described upper dentions matched one of the lowers there would be at least three species of *Priacodon* in the Morrison. *Priacodon* and other Morrison triconodonts are relatively large mammals for the formation.

Trioracodon

Marsh (1880) described *T. bisulcus* from Quarry 9, although he assigned the species to *Triconodon*. Simpson (1928) distinguished the specimen from *Triconodon* and gave it the new generic designation. He also recognized and named an additional species of *Trioracodon* from the Purbeck of England. The teeth of *Trioracodon* are similar to those of *Priacodon*, but there are only three molars, whereas *Priacodon* has four. Rougier et al. (1996) determined that *Trioracodon* and *Priacodon* form a monophyletic group along with *Triconodon*, which is known from England.

Aploconodon

Simpson (1925b) named *Aploconodon comoensis* from Quarry 9 based on a jaw fragment with two molars. The molars have particularly small accessory cusps.

Phascolotheridium

Simpson (1925b) named *Phascolodon gidleyi* from fragments of a jaw, with four molars, from Quarry 9. Cifelli and Dykes (2001) renamed it *Phascolotheridium* due to preoccupation of the name by a protistan. This species has accessory cusps that are about half the height of the main cusp.

Triconolestes

This new genus was named by Engelmann and Callison (1998) as *Triconolestes curvicuspis* and is a new triconodont from Rainbow Park.

Symmetrodonta

Amphidon

Simpson (1925a) named and described *Amphidon superstes* based on a lower jaw from Quarry 9. It is the only known specimen of this species and has "obtuse-angled" molars which are functionally monocuspid with small, indistinct accessory cusps (Simpson, 1929). The small size of the cusps, however, could be due to wear and/or preservation (Cassiliano and Clemens, 1979).

Tinodon

Marsh (1879c) described *Tinodon bellus* and, later, *T. lepidus*, based on lower jaw material from Quarry 9. *Tinodon* is an "acute-angled" symmetrodont and appears to be the lower jaws associated with *Eurylambda* (Crompton and Jenkins, 1967).

Eurylambda

Simpson (1929) named *Eurylambda aequicrurius* based on a maxilla with one molar from Quarry 9 which he had initially referred to *Amphidon* (1925a). Simpson (1929) noted that *E. aequicrurius* was a possible upper dentition of *Tinodon*, and Crompton and Jenkins (1967) concluded that this was very likely the case. Prothero (1981) seemed to follow this, although he kept the separate names for the sake of clarity in his cladistic analyses of upper and lower dentitions. McKenna and Bell (1997) listed *Eurylambda* as a junior synonym of *Tinodon*.

Dryolestoidea

Paurodontidae

Paurodon

Marsh (1887c) named *Paurodon valens* from a lower jaw from Quarry 9. This species has a relatively short, robust jaw and just six post-canine teeth.

Archaeotrigon

Simpson named *Archaeotrigon brevimaxillus* (1927) and *A. distagmus* (1929), both based on lower jaws from Quarry 9.

Tathiodon

This genus was named by Simpson (1927) and found at Quarry 9.

Araeodon

The specimen on which this genus is based was found in 1897 at Quarry 9 by the AMNH expeditions led by H.F. Osborn. The specimen was described and named by Simpson (1937).

Foxraptor

This genus is based on a specimen from the Breakfast Bench locality high in the Morrison at Como Bluff (Bakker et al., 1990; Carpenter, 1998b).

Euthlastus

This genus was named by Simpson (1927), on the basis of an upper dentition and considered a dryolestid. McKenna and Bell (1997) and Martin (1999) listed it as a paurodontid.

Pelicopsis

Yet another genus based on an upper dentition, this taxon, named by Simpson (1927) and identified as possibly a paurodontid by Simpson (1929), has been listed as a paurodontid by McKenna and Bell (1997).

Comotherium

This genus was found during the AMNH/YPM expedition to Quarry 9 in the late 1960s and named by Prothero (1981) based on an upper dentition. It was identified as a paurodontid by Martin (1999).

Dryolestidae

Dryolestes

This genus is monospecific and based on *D. priscus*, the type specimen of which (YPM 11820) was the first Jurassic mammal found in North America (Marsh, 1878e). The genus is known from Quarry 9, but the type specimen was collected by W.H. Reed in the vicinity of Quarry 5 at Como Bluff in May 1878 (Ostrom and McIntosh, 1966).

Amblotherium

A North American species of this small dryolestid genus was named by Marsh (1879c). Simpson (1927) named a second species, but Martin (1999) synonymized it with *A. gracilis*. The cusps of this genus are more pointed and erect than those of *Dryolestes*.

Kepolestes

This genus is based on a single lower jaw (USNM 2723) from the Marsh-Felch Quarry at Garden Park, Colorado. There are eight molars, but most are rather worn. The last molar is unique in being a simple peg, but Prothero (1981) noted that this may be due to abnormal development in this individual, so without any other specimens it is impossible to determine if this feature is autapomorphic for the genus. Martin (1999) listed *Kepolestes* as a junior synonym of *Amblotherium*.

Laolestes

This genus is represented by two species and was originally identified from Quarry 9 (Simpson, 1927, 1929). The teeth of the lower jaw are characterized by an internal cusp that is slightly split into two blunt processes.

Melanodon

This genus also has two species and was named from specimens found at Quarry 9 at Como Bluff (Simpson, 1927, 1929). It likely represents an upper dentition of *Laolestes* (Martin, 1999).

Malthacolestes

This is another genus named by Simpson (1927) as a dryolestid, although McKenna and Bell (1997) listed it as being synonymous with *Melanodon*. It is based on an upper dentition.

Herpetairus

This genus consists of two species named by Marsh (1879c) and Simpson (1929) from Quarry 9. The genus is considered to be the upper dention of *Dryolestes* by McKenna and Bell (1997) and by Martin (1999).

Miccylotyrans

This is a genus from Quarry 9, based on an upper dentition named by Simpson (1927).

ECOLOGICAL CATEGORIZATIONS

The following section details the variables and categories used to characterize each taxon in the Morrison Formation. The variables include locomotion/habitat, feeding mode, and mass. Specific taxa from the Morrison Formation are then categorized for each variable.

Categories and variables are based on Damuth et al. (1992); the Locomotion/Habitat variable in this study is a combination of Shelter and Feeding habitats and Locomotion variables in their table 4.1. Categories in this study are based on the same table but modified for what can be inferred for fossil genera from the Morrison Formation.

Locomotion/Habitat

Aquatic

Species that spend their lives entirely within bodies of water, including actinopterygian fish and lungfish. Jurassic lungfish would be in this category because they probably did not aestivate (Kirkland, 1987).

Semiaquatic

Species that either spend much of their time in water and some of it on land (turtles, crocodilians, and *Cteniogenys*) or are dependent on water sources (permanent or temporary) for reproductive parts of the life cycle (frogs and salamanders).

Terrestrial

Ground surface dwellers independent of water except for drinking, including all theropod, sauropod, and ornithischian dinosaurs.

Specialized Terrestrial

Fully terrestrial animals not dependent on more than drinking water but are generally small and probably adapted for some type of more specialized terrestrial locomotory mode. Because almost no associated postcranial elements are known for most small animals of the Morrison Formation (<1 kg), it is nearly impossible to determine specific habits, but it is likely that there were at least some scansorial and fossorial species among the mammals and small reptiles. This category is set up to distinguish them from other terrestrial animals, which were mainly dinosaurs.

Aerial

Species capable of flight.

Feeding Mode

Carnivore

Species that eat mainly other vertebrates; consumers of the second level or higher that include invertebrates as a significant

part of the diet are excluded. Theropod dinosaurs and crocodilians are the main members of this group, though young individuals of each may have fed on invertebrates as well. Carnivores are subdivided into Small, Medium, and Large carnivore categories: Small Carnivores are those under 50 kg, Medium Carnivores are those between 50 kg and 400 kg, and Large Carnivores are those above 400 kg.

Herbivore

Species that feed on plants. These species are subdivided into Low, Medium, and High Browsers. Low Browsers fed mainly at levels within 2 m of the ground surface, Medium Browsers fed mainly at levels below 4 m, and High Browsers fed mainly above 4 m.

Invertivore

Small species which needed high energy food and were likely too small to have ingested other vertebrates. Included are most of the mammals, the frogs and salamanders, and the lizards. These forms probably ate insects, grubs, and other soft-bodied and hard-bodied invertebrates.

Invertivore/Carnivore

Aquatic, semiaquatic, and terrestrial species that probably fed mostly on large to small invertebrates but also occasionally on smaller fish and/or vertebrates. Lungfish, for example, may have fed on fish, clams and snails, whereas smaller Invertivore/Carnivores probably fed on insects as well as small fish. On land, some species which fed largely on either insects or small vertebrates may have less often but not infrequently fed on the other group.

Omnivore

Species that fed on plant material as well as some invertebrates and possibly vertebrates, depending on the predator's size. Included in this category are turtles and some mammals.

Mass

Masses were estimated estimated in kilograms using the technique of Anderson et al. (1985) for most dinosaurs and by published estimates and comparisons with modern taxa for most non-dinosaurian taxa. Weights of crocodilians and turtles were partly based on estimates in Dodson et al. (1980).

OSTEICHTHYES

Amiiformes indet.

Morrolepis schaefferi

Hulettia hawesi

cf. *Leptolepis* sp.

Pycnodontoidea indet.

Locomotion/Habitat—All actinopterygian fish in the Morrison Formation were Aquatic.

Feeding Mode—Based on the preserved size, it is assumed that most of the fish ate invertebrates such as surface insects and worms as well as occasional smaller fish. Modern trout sometimes ingest pine needles and other plant material, but this is unlikely to be a major source of energy for fish of this size. The Morrison actinopterygians are classified as Invertivore/Carnivores.

Mass—Although some amioids may have grown larger, most remains found in the formation indicate that most individuals were small and weighed approximately 1 kg or less. Most preserved fish elements are fairly small and probably represent fish that weighed about 500 g, and this will be used as the average mass estimate for actinopterygians.

Dipnoi

***Ceratodus* sp.**

Ceratodus robustus

Locomotion/Habitat—*Ceratodus* is assumed to have been fully Aquatic and not to have aestivated, as no aestivation burrows are known from the Jurassic (Kirkland, 1987).

Feeding Mode—The teeth of Morrison lungfish indicate that the animals probably ate soft-bodied invertebrates when young and clams and other harder-shelled animals as adults (Kirkland, 1987). They may also have eaten some aquatic plant material and, when larger, some small fish and other vertebrates, as modern lungfish sometimes feed on these items. Thus, the *Ceratodus* specimens from the Morrison Formation are categorized as being Invertivore/Carnivores.

Mass—A live specimen of the African lungfish *Protopterus* at the University of Colorado has a skull size estimated to be similar to those of *Ceratodus* specimens that produced tooth plates of the size most often found in the Morrison. This *Protopterus* specimen is thus estimated to be about the size of most Morrison Formation lungfish and is 78.5 cm long and weighs approximately 3 kg.

Specimens of *C. robustus* consist of rather large tooth plates, and the animals were probably about twice as long as other species of *Ceratodus*. *C. robustus* is thus estimated to have had a mass of about 24 kg.

ANURA

Enneabatrachus

Rhadinosteus

Pelobatidae

Locomotion/Habitat—The mode of life for these species is classified as Semiaquatic due to the frogs' need for water sources and because many modern species live in or near lakes, swamps, marshes, and streams. Modern discoglossids and pelobatids, however, have varied habitat preferences ranging from highly aquatic or near temporary water to habitats in more arid regions (Mattison, 1987). Varied tolerance, if it were characteristic of Jurassic forms as well, would have been adaptive, considering the semi-arid environments that may have been prevalent for much of the time of Morrison deposition (Turner and Fishman, 1991). This may help explain the relative rarity of frogs in collections from the Morrison Formation.

Feeding Mode—Many small frogs are Invertivores and eat mainly ants, termites, beetles, snails, and worms (Mattison, 1987), all of which appear to have been present during Morrison times.

Mass—The small size of most Morrison frog material, and comparison with estimates of similarly small mammalian specimens, as well as similar-sized modern frogs, indicate that the animals were about 100 g in weight.

CAUDATA

Caudata indet.

Locomotion/Habitat—Modern salamanders exhibit a range of life histories and live in a variety of envrionments. Some species take several years to metamorphose, whereas others do so completely within the egg, and some species are entirely aquatic as adults, whereas more than half of modern species are terrestrial as adults and return to water sources mainly to reproduce (Hairston, 1987). Field observations and experiments indicate that pond-dwelling species occur only in areas devoid of predatory fish and that predation is more a factor in driving species to become terrestrial than is competition (Hairston, 1987). Many species live in temporary ponds, and this, together with the fact that

predatory fish seem to have been present in at least some aquatic environments in the Morrison, suggests that salamanders from the Morrison Formation were probably largely terrestrial. Some modern tiger salamanders spend much of their time in mammal burrows (Trenham, 2001). Considering the animals' dependence on sources of water, however, they will not be classified as being fully terrestrial for this study but rather as Semiaquatic.

Feeding Mode—Modern salamanders eat a variety of small crustaceans in aquatic habitats and insects and other small invertebrates in terrestrial environments (Hairston, 1987). Those from the Morrison will therefore be categorized as Invertivores.

Mass—All specimens are small enough to indicate animals less than 1 kg and were estimated as being about 100 g.

REPTILIA

Chelonia

Glyptops

Dinochelys

Uluops

Dorsetochelys

Locomotion/Habitat—All Morrison Formation turtles are Semiaquatic species.

Feeding Mode—The turtles are classified as Omnivores, as modern chelonians eat insects, small fish and other vertebrates, and plant material, and some vary their diet seasonally and/or with age (Alderton, 1988). Demuth and Buhlmann (1997) found that one form of modern turtle is largely insectivorous but also ate some mollusks and vertebrates, and Pérez-Emán and Paolillo (1997) studied the diet of a modern turtle that was mainly herbivorous but also ate some fish and invertebrates. Neither of these forms, however, changed diet ontogenetically. Population densities of largely insectivorous modern species of turtles seem to be lower in more permanent bodies of water where there is significant competition from insectivorous fish.

Mass—Based on their relatively small size, turtles from the Morrison Formation probably weighed 1–10 kg. Dodson et al. (1980) estimated the weight of *Glyptops* at 5–10 kg. For this study, the estimated mass of the adult turtles is 5 kg.

Sphenodontia

Opisthias

Theretairus

Locomotion/Habitat—These forms, similar to the modern *Sphenodon*, are land-dwelling and for this study considered of the Specialized Terrestrial category, as they may have been ground-dwelling, fossorial, scansorial, or arboreal.

Feeding Mode—The triangular teeth and small size of these animals suggest that they were largely insectivorous. Cooper (1994) noted that the modern *Sphenodon* is probably an ambush predator of insects, and thus *Opisthias* and *Theretairus* will be considered Invertivores for this study.

Mass—These forms were small and probably weighed about 100 g.

Eilenodon

Locomotion/Habitat—Specialized Terrestrial.

Feeding Mode—This genus has rather large, blunt teeth and has been described as herbivorous (Rasmussen and Callison, 1981a). Assuming it was not a canopy-dwelling arboreal form and stayed within a few meters of ground level, it would have been a Low Browser.

Mass—Jaws of this animal were relatively large and some adults may have approached 1 kg in weight, but most individuals are estimated to have weighed 500 g.

Lacertilia

Parviraptor

Dorsetisaurus

Paramacellodus

Saurillodon

Schilleria

Locomotion/Habitat—All five known genera of lizards from the Morrison Formation are considered to be Specialized Terrestrial and some may have been scansorial.

Feeding Mode—These lizard genera are categorized as Invertivores, as most small, modern skinks and anguids are largely insectivorous (Mattison, 1989; Cooper, 1994).

Mass—Based on the small size of all the known specimens, the lizards of the Morrison are estimated to have weighed approximately 100 g.

Serpentes

Boidae?

Locomotion/Habitat— Remains of Morrison snakes are rare and known from few parts of the skeleton. The only known elements are from the Fruita Paleontological Area and a possible snake tooth from Rainbow Park in Dinosaur National Monument. However, as this is the earliest known snake taxon and it may have had vestigal limbs (J. Kirkland, pers. comm., 1997), it is likely that the snake from the Morrison was Specialized Terrestrial.

Feeding Mode—By comparison with modern forms, it is assumed that the Morrison snake was a Small Carnivore and probably fed on mammals and possibly lizards and other small vertebrates.

Mass—With so little of the skeleton known it is difficult to determine the mass of the animal, but for this study it is estimated to have weighed 500 g.

Choristodera

Cteniogenys

Locomotion/Habitat—Like turtles and crocodilians, *Cteniogenys* was probably Semiaquatic (Evans, 1990).

Feeding Mode—Based on its small size (about 25 cm total length) and small, conical teeth, *Cteniogenys* probably ate insects and very small fish, and thus is categorized as an Invertivore/Carnivore.

Mass—*Cteniogenys* is a small animal, approximately 25 cm long (Evans, 1991), and probably weighed about 200 g.

Crocodylia

"Fruitachampsa"

Hallopus

Locomotion/Habitat—The long slender limbs of these forms indicate that they were Terrestrial and probably cursorial (Walker, 1970; Clark, 1985; Kirkland, 1994).

Feeding Mode—The sharp teeth of *"Fruitachampsa"* suggest a carnivorous diet. Kirkland (1994) suggested that terrestrial crocodilians may have scavenged nests of dinosaurs as part of their diet; other possible dietary items include mammals, lizards, and other small vertebrates. Although no cranial elements of *Hallopus* are known, it is probable that it was similar to other crocodilians in being carnivorous. These crocodilians are thus categorized as Small Carnivores.

Mass—The skull and skeleton of *"Fruitachampsa"* indicate an animal about the size of a large house cat. Based on this comparison, these crocodilians probably weighed about 5 kg. *Hallopus* was of similar size.

Hoplosuchus

Locomotion/Habitat—This specimen is too poorly preserved to be certain of its relationships, but it appears to have had relatively long limbs and was thus considered Terrestrial for this study.

Feeding Mode—*Hoplosuchus* was presumably Carnivorous.

Mass—*Hoplosuchus* is very small, but the available specimen may be a juvenile, as the orbits are particularly large. Assuming that it is an adult, it would have weighed less than 1 kg. If it is a juvenile there is no telling what the average adult size would have been, but it may have been in the 1–10 kg range. The preserved specimen represents an individual that probably weighed about 200 g.

Goniopholis

Eutretauranosuchus

Macelognathus

Locomotion/Habitat—As goniopholid crocodilians are similar in overall form to modern crocodilians, and as their remains by far more common in aquatic environments, these forms will be categorized as Semiaquatic.

Feeding Mode—These Morrison crocodilians are categorized as Medium Carnivores. Though young crocodilians may feed largely on insects, animals of the lengths indicated by the material from most Morrison sites probably fed primarily on fish, but also on some small reptiles, mammals, and dinosaurs. The modern crocodilian *Crocodylus niloticus*, at lengths of 2.5–3 m, feeds mostly on fish, but also eats small mammals and reptiles, and occasionally ingests snails and shellfish (Pooley, 1989).

Mass—The preserved elements of Morrison goniopholid crocodilians indicate animals of relatively moderate size that most probably weighed less than 100 kg. Dodson et al. (1980), based on Mook's (1925, 1942) descriptions, estimated the weight of *Goniopholis* as being up to 50–60 kg. *Eutretauranosuchus* (Mook, 1967) probably weighed about the same, as the type specimen (CMNH 8028), though apparently not fully grown, is slightly smaller than several known *Goniopholis* specimens. The mass estimate for these crocodilians used in this study will be 55 kg.

Pterosauria

Comodactylus

Dermodactylus

Mesadactylus

Kepodactylus

Locomotion/Habitat—The occurrence of pterosaur trackways in the Tidwell and Salt Wash members indicates that Morrison pterosaurs spent at least part of their time walking in sandy shoreline and stream environments. Obviously, however, these animals were adapted for flight, and the muscle attachments for the sternum and humerus appear to indicate that many pterosaurs were capable of powered and soaring flight. All of the Morrison Formation genera are thus categorized as Aerial, and though several purported birds have been reported from the formation (Marsh, 1881b; Jensen, 1981), the pterosaurs remain the only known, unquestionable flying vertebrates from the formation, as all Morrison "birds" appear to be indeterminate pterosaurs.

Feeding Mode—Stomach contents of several genera of pterosaurs from Europe, including *Pteranodon* and *Rhamphorhynchus*, indicate that these animals fed largely on fish (Wellnhofer, 1991). Long, sharp, conical teeth in the uncataloged collections from Quarry 9 at the National Museum of Natural History have been identified as pterosaurs and resemble the teeth of *Rhamphorhynchus*. The pterosaurs from the Morrison Formation will be categorized as Small Carnivores.

Mass—Wellnhofer (1991) estimated the weight of the pterodactyloid *Pteranodon* as approximately 16.6 kg. Based on this estimate, and scaling for their respective estimated wingspans, the estimated masses of the Morrison pterodactyloids are: *Kepodactylus*, 6.0 kg; *Mesadactylus*, 3.3 kg; and *Dermodactylus*, 3.3 kg. Wellnhofer's (1991) estimate for the rhamphorhynchoid *Rhamphorhynchus* was 0.48 kg, which gives an estimate for *Comodactylus* of 1.4 kg. Thus, all the pterosaurs in this study are in the 1–10 kg category.

Dinosauria

Theropoda

Ceratosaurus

Allosaurus

Saurophaganax

Torvosaurus

Edmarka

Locomotion/Habitat—All five genera of large theropods considered in this study are fully Terrestrial.

Feeding Mode—All are also considered Large Carnivores, as teeth in each are large, recurved, and serrated.

Mass—*Allosaurus* has been estimated as having had a modal adult body mass of 1500 kg (Dodson et al., 1980), 1000–4000 kg (Peczkis, 1994 based on the method of Anderson et al., 1985), or 1010 kg (Paul, 1988a). Paul's (1988a) estimate is used here, although larger specimens, including *Epanterias*, may have reached as much as 1950 kg. *Torvosaurus* and the similarly sized (and possibly synonymous) megalosaurid *Edmarka* are estimated at 1950 kg (Paul, 1988a). *Saurophaganax* may have weighed as much as 2720 kg (Chure, 1995). Dodson et al. (1980) put the mass of *Ceratosaurus* at about 1000 kg, although Peczkis (1994) estimated 400–700 kg. Paul's (1988a) estimate, used here, is 524 kg.

Marshosaurus

Stokesosaurus

Locomotion/Habitat—Both forms are fully Terrestrial.

Feeding Mode—Teeth for both genera are sharp and serrated, like most theropod teeth, and thus indicate carnivorous diets. These taxa comprise the Medium Carnivore category.

Mass—Paul (1988a) estimated about 225 kg for the mass of *Marshosaurus*, whereas Peczkis (1994) estimated 100–400 kg. The median weight of 250 kg will be used in this study. Paul (1988a) estimated a mass of about 80 kg for *Stokesosaurus*. Peczkis (1994) estimated 70–100 kg; a mass of 85 kg is used here.

Coelurus

Ornitholestes

Koparion

Locomotion/Habitat—All small theropods are considered fully Terrestrial.

Feeding Mode—All of these forms are considered Small Carnivores. Teeth of *Ornitholestes* and the troodontid *Koparion* are serrated and indicate carnivorous diets (although Holtz et al. [1994] suggested that troodontids may have been omnivorous). *Coelurus* is presumably carnivorous based on similarity to other small theropods.

Mass—Because *Koparion* is based on a single tooth, it is difficult to estimate its mass. By comparison with *Troodon*, however, it may have weighed 10–40 kg (Peczkis, 1994). Paul (1988a) estimated the weights of troodontids as 13–50 kg, depending on the species. *Koparion* is a small tooth and may have come from a fairly small animal so the lower end of this estimate (13 kg) will be used as the mass. Paul's (1988a) estimate of 20 kg will be used for

Coelurus. Peczkis's (1994) estimate for the mass of *Ornitholestes* is 10–40 kg; Dodson et al. (1980) had 20 kg. Paul's (1988a) estimate is significantly lower at 12.6 kg but will be used here for consistency.

Elaphrosaurus

Locomotion/Habitat—*Elaphrosaurus* was fully Terrestrial.

Feeding Mode—Without skull material or even much of the skeleton, it is difficult to determine the probable diet of *Elaphrosaurus*. This form has traditionally been considered a primitive ornithomimosaur (Barsbold and Osmólska, 1990), though in most recent studies it has been removed from this group (Holtz, 1994). Most ornithomimids are edentulous and may have been carnivorous (Barsbold and Osmólska, 1990) or omnivorous (Russell, 1972; Osmólska et al., 1972). Even if it were a primitive ornithomimosaur, *Elaphrosaurus* probably had teeth, as *Pelecanimimus* had many small teeth in its jaws (Pérez-Moreno et al., 1994). The skull of *Elaphrosaurus* may have been ornithomimosaur-like with small teeth, and been adapted for a diet of small vertebrates and insects, or it may have been larger, with larger teeth, and adapted for a more strictly carnivorous diet. For this study, *Elaphrosaurus* will be considered to have been mostly carnivorous and thus a Medium Carnivore.

Mass—Peczkis (1994) estimated the mass of *Elaphrosaurus* at 100–400 kg, and Paul (1988a) estimated 210 kg, a figure which will be used in this study.

Sauropoda

Brachiosaurus

Camarasaurus

Locomotion/Habitat—The sauropod genera in this study are considered fully Terrestrial, as the adaptations and structural morphology of the animals indicate that they lived on land and were not dependent on water for physical support (Bakker, 1971; Coombs, 1975).

Feeding Mode—Both *Brachiosaurus* and *Camarasaurus* are considered High Browsers in this study and probably fed at levels 3–5 m above the ground and higher. It is plausible that these taxa occasionally fed below this level, as giraffes today can reach up to 5 m into trees but also feed below 2 m (Dagg and Foster, 1976). If the neck of *Brachiosaurus* was not held at a high, nearly vertical angle (after the work of K. Stevens and M. Parrish versus Paul [1988c]), the head would have been well above the ground. The high shoulder region and long humerus, as well as the long neck of *Brachiosaurus* indicate it was adapted for feeding on high foliage, and estimates based on scaled reconstructions by Greg Paul (in McIntosh et al., 1997), adjusted for a less vertical neck position (after the work of Stevens and Parrish [1996, 1997, 1999]), indicate that the neck position for *Brachiosaurus* may have been some 9.4 m above the ground. Although *Camarasaurus* is smaller and did not have as long a neck, it too appears to have fed on higher, tougher vegetation; the head height estimate for *Camarasaurus*, based on the same reconstructions, is about 5.7 m. The relatively large teeth of these kinds of sauropods may have been useful for the tougher vegetation. One indication of possible high browsing by *Camarasaurus* is the differences between microwear patterns of adult and juvenile specimens of this genus and adult *Diplodocus*. Adult *Camarasaurus* show rougher microwear than juvenile *Camarasaurus* and adult *Diplodocus* (Fiorillo, 1998), which may suggest that juvenile *Camarasaurus* had dietary overlap with *Diplodocus* until reaching adult size, at which time they began feeding at higher levels in the canopy. Teeth of *Brachiosaurus* and *Camarasaurus* indicate different chewing styles; *Brachiosaurus* possessed a more slicing tooth action, whereas the thick teeth of *Camarasaurus* contacted directly and thus resulted in a degree of oral processing of food (Calvo, 1994). It has been suggested that the finer microwear of *Diplodocus* was a result of its feeding consistently at higher levels away from silica grains in the leaves (Calvo, 1994), but the similarity between *Diplodocus* microwear and that of obviously low-feeding juvenile *Camarasaurus* is still difficult to explain.

Mass—For the sauropods, the technique of Anderson et al. (1985) was used to determine weight estimates, and these were compared to other studies. My measurements of *Brachiosaurus altithorax* (FMNH 25107) give an estimate of 43,896 kg. Other studies, sometimes based on the Tanzanian *B. brancai*, have estimated the weight as 46,600 kg (Alexander, 1989); 87,000 kg (Colbert, 1962); 54,500 kg (Coe et al., 1987); 10,000–40,000 kg (Peczkis, 1994); and 31,600 kg (Anderson et al., 1985). Interestingly, the last three estimates all used the same technique of Anderson et al. (1985). For this study, the estimate of 43.9 metric tonnes will be used.

Measurements of *Camarasaurus* give a range of mass estimates, as the sizes of the animals preserved with both the humerus and femur intact (necessary for the method) differ greatly in size. Measurements of the average-sized YPM 1901 give a weight estimate of 9321 kg and measurements of the moderately large SDSM 351 give 18,413 kg. The estimate used in this study will be a nearly-median 14,000 kg. Specimens of *C. supremus* can be up to 50% larger than an average *Camarasaurus* in linear dimensions, which would result in an animal weighing more than three times as much, or up to 47,000 kg.

Diplodocus

Barosaurus

Apatosaurus

Supersaurus

Seismosaurus

Locomotion/Habitat—All were Terrestrial.

Feeding Mode—All of these diplodocids, except *Seismosaurus* and *Supersaurus*, are considered Medium Browsers and probably fed mainly from ground level up to 3–5 m. Microwear patterns of *Diplodocus*, which presumably had teeth similar to the others, indicate that the animal fed on softer vegetation than adult *Camarasaurus* (Fiorillo, 1998), and the feeding mechanism of *Diplodocus* appears to have been adapted for a range of vegetation (Barrett and Upchurch, 1994). Stevens and Parrish (1996, 1997, 1999) computer-modeled sauropod cervical vertebrae articulation and determined that both *Diplodocus* and *Apatosaurus* had neutral neck positions within a meter or two of the ground. My estimates based on Paul's reconstructions indicate approximate head heights of 2.9 m for *Diplodocus*, 3.4 m for *Apatosaurus*, and 4.6 m for *Barosaurus*. Stevens and Parrish (1997) also calculated that the maximum heights possible for the necks of *Diplodocus* and *Apatosaurus* at 3.8 m and 5.3 m, respectively. The unusual amount of ventriflexion apparently possible in *Apatosaurus* and *Diplodocus* may have been an adaptation for some tripodal feeding (Stevens and Parrish, 1997), but I do not believe this would have been as habitual a feeding mode as proposed by some. Some of the purported adaptations for a tripodal feeding stance in diplodocids such as heightened sacral vertebral spines and relatively short front limbs could simply be, respectively, adaptations for relatively lengthened cervical and caudal series and inherited primitive conditions.

The head height levels for diplodocids as calculated here and by Stevens and Parrish (1997) are noticeably lower than those for *Camarasaurus* and *Brachiosaurus* and this, along with the difference in microwear between adult *Diplodocus* and *Camarasaurus* and the apparent overlap between juvenile *Camarasaurus* and adult

Diplodocus diets, is taken to indicate lower browsing heights for diplodocids.

Because they were considerably larger than other diplodocids and thus would have had higher overall head heights, *Seismosaurus* and *Supersaurus* are considered High Browsers.

Mass—Using my measurements and the method of Anderson et al. (1985) the weights of these diplodocids were calculated as: 12,657 kg for *Diplodocus*, based on USNM 10865; 24,247 kg for *Apatosaurus*, based on YPM 1980 (*A. louisae*, CM 3018, is significantly heavier at 34,035 kg); 11,957 kg for *Barosaurus*, based on AMNH 6341; and 40,200 kg for *Supersaurus* and 42,500 kg for *Seismosaurus*, based on the fact that these animals are roughly similar to *Barosaurus* and *Diplodocus*, respectively, in overall shape but may be approximately 50% larger in linear dimensions (Gillette, 1991). Curtice (pers comm., 2002) noted that, compared to the largest known *Diplodocus*, *Seismosaurus* caudals are not as unusually large as previously thought so that the animal may be only 25% longer and thus would weigh closer to 24,000 kg.

Previous estimates for some of these genera include 25,000 kg for *Apatosaurus*, 10,000 kg for *Diplodocus*, and 25,000 kg for *Barosaurus* (Dodson et al., 1980) and 10,000–40,000 kg for *Apatosaurus*, *Diplodocus*, and *Barosaurus* (Peczkis, 1994). Coe et al. (1987) used the same method of Anderson et al. (1985) and got 16,000 kg for *Diplodocus*, 42,500 kg for *Apatosaurus*, and a staggering 40,000 kg for *Barosaurus*. The differences in estimations here are difficult to explain, but Coe et al. (1987) did not specify the specimens used. It seems impossible that *Barosaurus* could have weighed that much more than *Diplodocus*, an animal to which it is similar in both size and relative slenderness (despite reports of significantly greater size in *Barosaurus*).

Haplocanthosaurus

Locomotion/Habitat—Terrestrial.

Feeding Mode—No skull is known from any specimen of *Haplocanthosaurus*, but, like all sauropods, it was undoubtedly an herbivore. Between the lack of cranial material or even teeth and the incompleteness of known skeletons, it is difficult to determine the browsing level. If Paul's reconstruction in McIntosh et al. (1997) is reasonably accurate, the head height may have been approximately 3.9 m, thus making it a Medium Browser.

Mass—The weight of this animal is also difficult to determine, as no good associated humerus/femur sets are known. The only published weight estimation is 7,000 kg by Coe et al. (1987) and this must be based on *H. priscus*, the species known from the Marsh-Felch Quarry which, though fully adult, is a fairly small sauropod. *H. delfsi*, from the Cleveland Quarry, is linearly 35–50% larger (McIntosh and Williams, 1988), which results in mass estimates for this species of 17,222 kg to 23,625 kg. The lower of these two will be used for this study, and for specimens closer to the size of *H. priscus*, the 7,000 kg estimate will be used.

Dystrophaeus

Locomotion/Habitat—Terrestrial.

Feeding Mode—This genus is known only from the Tidwell Member of eastern Utah. Though the animal is still quite poorly known, it appears similar to diplodocids to some degree (McIntosh, 1990a). It will thus be considered a Medium Browser.

Mass—By comparison with similarly slender diplodocids, it is estimated to have weighed approximately 12,000 kg.

Ornithischia

Stegosauria

Stegosaurus

Hesperosaurus

Locomotion/Habitat—Both forms are fully Terrestrial. *Stegosaurus* possibly preferred upland areas or areas further from water than sauropods (Dodson et al., 1980).

Feeding Mode—The teeth of *Stegosaurus* indicate that it and its relatives were herbivorous. The head of *Stegosaurus* was held within a little over a meter of the ground (Galton, 1990, 1997), and though it probably could have fed tripodally, that is not considered a major feeding strategy for this study. The stegosaurs from the Morrison Formation are thus considered Low Browsers.

Mass—The mass of *Stegosaurus* has been estimated as 4,000–7,000 kg (Peczkis, 1994), 5,000 kg (Bakker, 1980), and 2,000 kg (Dodson et al., 1980). Measurements of DMNH 1483 (*S. stenops*) give a mass estimate, used for this study, of 5,284 kg. *Hesperosaurus* is estimated to have weighed about 5000 kg.

Ankylosauria

Mymoorapelta

Gargoyleosaurus

Locomotion/Habitat—Ankylosaurs are generally agreed to have been Terrestrial.

Feeding Mode—With teeth somewhat similar to stegosaurs, the ankylosaurs were herbivorous and had head height similar as well, at about 1 m above ground level. They are thus Low Browsers.

Mass—These genera are similar in size, and their size comparison with other smaller-sized, early ankylosaurs indicates a probable weight of about 1,000 kg (Peczkis, 1994). Measurements based on Mygatt-Moore and Hups Quarry specimens suggest a similar weight.

Ornithopoda

Heterodontosauridae?

cf. *Echinodon*

Locomotion/Habitat—This is a bipedal, Terrestrial animal.

Feeding Mode—With teeth similar in some ways to those of other small ornithopods, *Echinodon* was most likely a herbivore, and considering its small size, is a Low Browser.

Mass—The animal probably weighed about 5 kg.

Othnielia

Drinker

Dryosaurus

Camptosaurus

Locomotion/Habitat—All of these ornithopod genera were Terrestrial.

Feeding Mode—Teeth of *Othnielia* and *Drinker* were simple and leaf-shaped but adapted for herbivorous browsing; *Dryosaurus* teeth and *Camptosaurus* teeth are similar to those of iguanodontids and also adapted for feeding on plants. All four fed within a meter or two of the ground and are thus Low Browsers.

Mass—Estimates of the mass of *Drinker* and *Othnielia* range from 4 kg to 20 kg (Dodson et al., 1980; Peczkis, 1994). Probably most adult individuals of each of these small genera weighed just under 10 kg and thus were in the 1–10 kg category. Estimates of the weight of *Dryosaurus* include 100–400 kg (Peczkis, 1994) and a modal weight of 100 kg (Dodson et al., 1980). For this study, measurements of YPM 1876 (*D. altus*) were used with the method of Anderson et al. (1985) to estimate an adult weight and gave 114 kg. Previous estimates for *Camptosaurus* are 500 kg (Bakker, 1980), 700 kg (Dodson et al., 1980), and 400–700 kg (Peczkis, 1994). My measurements of *Camptosaurus* specimens YPM 1877 and YPM 1880 give weights for this genus of 785 kg and 874 kg, respectively. For this study, 830 kg, the mean of these two estimates, was used.

MAMMALIA

Docodonta

Docodon

Locomotion/Habitat—*Docodon* is considered a Specialized Terrestrial animal. Lillegraven and Krusat (1991) suggested that the Portugese docodont *Haldanodon* was fossorial, and *Docodon* may have been as well.

Feeding Mode—Docodonts appear to have been Omnivores and to have eaten at least some plant material in addition to small invertebrates (Kron, 1979). The multiple cusps of docodonts have numerous shearing surfaces, which would be useful in processing small, soft-bodied invertebrates and adult insects, but the teeth overall have relatively shorter, blunter cusps and greater occlusal surface area than most other Jurassic mammals, other than multituberculates, and these features probably allowed for greater flexibility of diet and for inclusion of small seeds and other plant material.

Mass—Bakker (1980) indicated that almost all early mammals were less than 100 g in weight. This estimate is used for most mammals here as well. Some species may have weighed slightly more or less but this seems like a reasonable average estimate, as jaws of most mammalian specimens from the Morrison Formation are about 25 mm in length.

Multituberculata

Ctenacodon

Psalodon

Zofiabaatar

Glirodon

Locomotion/Habitat—Multituberculates are considered Specialized Terrestrial, and though some multituberculates may have been scansorial, there is no evidence of any being fossorial or aquatic (Clemens and Kielan-Jaworowska, 1979).

Feeding Mode—The diet of multituberculates has been debated, though it is generally agreed they were herbivorous to some degree. Simpson (1926c) concluded that plagiaulacoid and ptilodontoid multituberculates were largely herbivorous. Krause's (1982) study of *Ptilodus* indicated that this genus and ptilodontoids generally were probably omnivorous. *Ptilodus* is not much larger than the Morrison multituberculate taxa, and though it has a single, larger blade-like p4, *Ptilodus* has a fairly similar lower dention to *Ctenacodon* and *Psalodon*, which have four, smaller, interlockling blade-like premolars. Krause (1982) also noted that ptilodontoids were probably too small to be entirely folivorous. Clemens and Kielan-Jaworowska (1979) concluded that, with the exception of taeniolabidids, multituberculates were omnivorous and fed on plant material and various invertebrate prey items when available. It is most likely, then, that Morrison multituberculates were Omnivores and ate a variety of plant material and seeds as well as insects and other small invertebrates.

Mass—100 g.

Triconodonta

Priacodon

Trioracodon

Aploconodon

Phascolotheridium

Triconolestes

Locomotion/Habitat—Triconodonts are categorized as Specialized Terrestrial animals and may have been scansorial, fossorial, or possibly ground-dwelling.

Feeding Mode—According to Jenkins and Crompton (1979), the association of triconodont fossils with bay and lagoon sediments in some areas, along with tooth comparisons to marine mammals, led some to speculate that triconodonts were piscivorous. However, the cusp morphology of these animals indicates that early forms may have fed on invertebrates, possibly including insects, larvae, and worms, and some later and larger triconodonts may have become at least partly carnivorous (Jenkins and Crompton, 1979; Cifelli and Madsen, 1998). Thus, for this study, the triconodonts will be considered Invertivore/Carnivores.

Mass—150 g. A slightly higher estimate is used here for the Triconodonta because many of the preserved jaws from the Morrison indicate animals slightly larger than other Morrison mammals.

Symmetrodonta

Amphidon

Tinodon

Locomotion/Habitat—Symmetrodonts are considered Specialized Terrestrial, as they may have been scansorial, ground-dwelling, or possibly fossorial, although almost no postcranial elements are known to help resolve this question.

Feeding Mode—The teeth of symmetrodonts were adapted for slicing and have several shearing surfaces. This is likely for breaking up prey such as small invertebrates and not for plant material (Cassiliano and Clemens, 1979). Symmetrodonts are thus categorized as Invertivores.

Mass—100 g.

Dryolestoidea

Paurodontidae

Paurodon

Archaeotrigon

Tathiodon

Araeodon

Foxraptor

Pelicopsis

Euthlastus

Comotherium

Locomotion/Habitat—Paurodontids are considered Specialized Terrestrial. There is some indication that these genera and/or dryolestids may have been scansorial or arboreal, as an articulated eupantothere postcranial skeleton from Portugal shows well-developed claws on the digits (Henkel and Krebs, 1977).

Feeding Mode—The high cusps and many shearing surfaces of the paurodontids indicate a diet of small invertebrates (Simpson, 1933; Kraus, 1979), and these genera are thus categorized as Invertivores.

Mass—100 g.

Dryolestidae

Dryolestes

Amblotherium **(Including** *Kepolestes***)**

Laolestes **(Including** *Melanodon* **and** *Malthacolestes***)**

Miccylotyrans

Locomotion/Habitat—Dryolestids are considered Specialized Terrestrial. The single eupantothere postcranial skeleton that shows well-developed claws on the digits suggests that paurodontids, and possibly dryolestids as well, were scansorial or arboreal (Krebs, 1991).

Feeding Mode—The noticeably high cusps of the dryolestids indicate a diet of small invertebrates (Simpson, 1933; Kraus, 1979), and these genera are thus categorized as Invertivores.

Mass—100 g.

RESULTS AND DISCUSSION

Taphonomic Characteristics

Abundance vs. Mass

The analysis of community structure preservation resulted in four graphs of Log_{10} weight by Log_{10} abundance. One graph each with abundances uncorrected (Fig. 15); with mammalian abundances corrected by a factor of ten (Fig. 16); with mammals (X10), small theropods (X7), ornithopods, theropods, and pterosaurs (X5), and stegosaurs and ankylosaurs (X3) corrected and other animals and the sauropods not corrected (Fig. 17); and with all dinosaurs and mammals corrected by a factor of ten (Fig. 18).

Figure 15 shows uncorrected abundance values, and the fitted trendline for this distribution has a slope of –0.43, which is far below the expected range for modern mammalian communities of –1.30 to –0.80 (Damuth, 1982). The distribution in which mammals are corrected to be tachymetabolic and dinosaurs are corrected to have "intermediate" metabolisms results in a slope of –0.53 (Fig. 17), and with a correction of only mammalian taxa the slope is –0.58 (Fig. 16). Both of these are a little closer to the expected slope. It is interesting that leaving all dinosaur taxa poikilothermic and correcting only the mammals results in what might appear to be a more realistic distribution. The evidence in favor of some type of elevated metabolism in at least some dinosaurs, however, is compelling, and the –0.53 slope of the distribution in Figure 17 is not much lower than the graph in which only mammals are corrected. The fully tachymetabolic correction in all dinosaurs results in a rather unrealistic positive slope (Fig. 18) that indicates either severe taphonomic bias in favor of large species, which is barely corrected for by Dale Russell's (1989; in Coe et al., 1987) method using the Behrensmeyer et al. (1979) study, or a very odd paleocommunity in which animals four orders of magnitude larger than the smallest forms are an order of magnitude more abundant.

Modern communities of mammalian and non-mammalian animals in a number of environments show a similar distribution when population densities are plotted on mass. These distributions have an average slope of –0.75 (Damuth, 1987), so the range found by Damuth (1982) should be similar in non-mammalian communities. The relatively flatter slopes in graphs of Morrison Formation taxa may be a result of either a taphonomic bias in favor of larger species that is not fully corrected for by the method used here and by Russell (1989; in Coe et al., 1987) or a result of a real difference between the Morrison paleocommunity and modern communities. Most likely the difference is due to a combination of these factors. The Behrensmeyer et al. (1979) taphonomic study that Russell's method was based on included animals up to

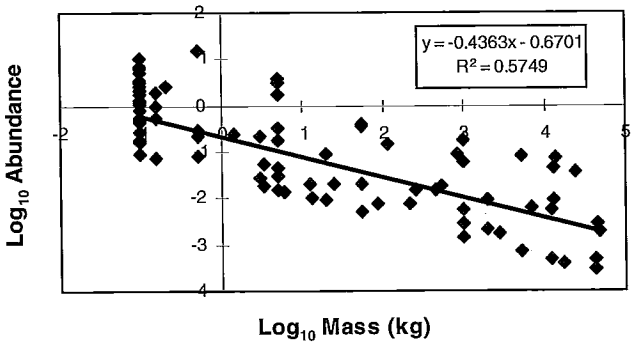

FIGURE 15. Unadjusted abundance versus mass distribution for individual Morrison Formation vertebrate taxa. Slope of the line (–0.436) is less than observed in most modern communities (Damuth, 1982).

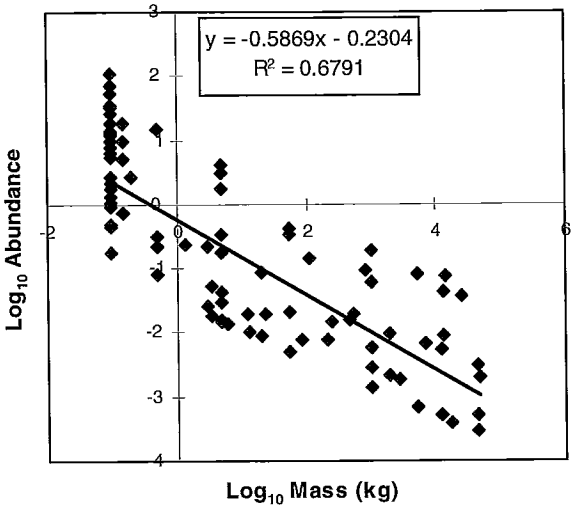

FIGURE 16. Abundance versus mass distribution for individual Morrison Formation vertebrate taxa, with observed abundances of mammalian genera increased by a factor of ten to adjust for presumed physiological differences.

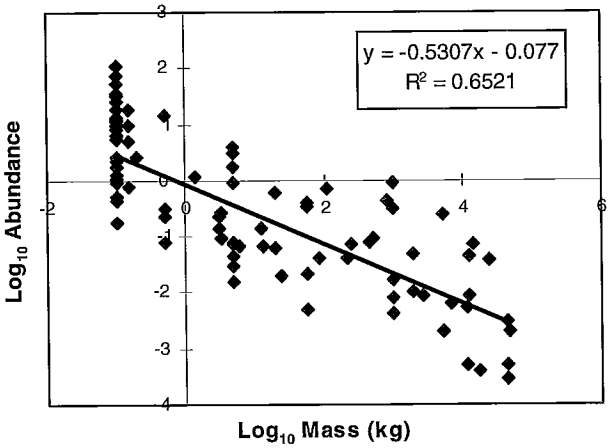

FIGURE 17. Abundance versus mass distribtuion for individual Morrison Formation vertebrate taxa, with the following abundances increased: mammals (X10), small theropods (X7), ornithopods, theropods, and pterosaurs (X5), and stegosaurs and ankylosaurs (X3). Sauropod dinosaurs and other animals were not adjusted.

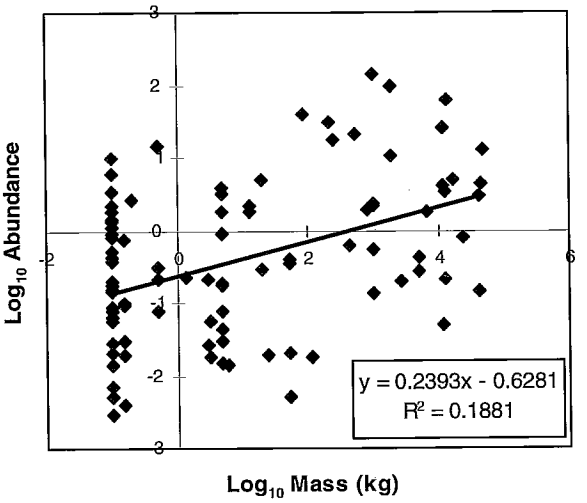

FIGURE 18. Abundance versus mass distribution for individual Morrison Formation vertebrate taxa, with all dinosaur and mammal abundances increased by a factor of ten. Note positive slope.

only 6300 kg and the extrapolation of the regression to animals close to an order of magnitude heavier is probably risky. Presumably, however, because it is the only way to currently correct for pre-burial taphonomic bias, the method should improve the relative abundances to more realistic levels. It would not be surprising either if the Morrison Formation vertebrate paleocommunity were significantly different from anything observed today. A greater diversity of animals with masses far greater than in any land ecosystem today, or even since the Jurassic, suggests that we should not necessarily expect the abundance distributions of different-sized animals to be similar to what we observe today. The apparently relatively greater abundance of large animals in the Morrison has been perplexing to a number of authors as it implies that we have either overestimated caloric requirements of the herbivorous dinosaurs or underestimated the regenerative capacity of the plants (Coe et al., 1987; Farlow, 1987; Tiffney, 1997). The data presented here only indicate that the abundances of the larger dinosaurs probably were greater than would be expected for a modern community and that this greater abundance probably had a significant influence on the diversity and abundance of smaller-bodied groups and may have resulted in significant habitat modification.

Group Occurrence and Sample Size

Plots of the number of localities (with different sample sizes) at which certain vertebrate groups occur (Figs. 19–20) were made to determine the most commonly found groups regardless of quarry sample size and to see if certain minimum sample levels were needed to find some groups. Among dinosaurs, the sauropods were by far the most commonly found animals when sites had only one specimen. Sauropods and theropods occurred almost equally at the most sites with two to five specimens. Interestingly, all dinosaur groups except ankylosaurs are found at at least a few single-specimen localities, and even a single-specimen mammal locality is known. The main trend in Figure 19 indicates that the most commonly preserved dinosaur groups are sauropods, then theropods, then stegosaurs and ornithopods, with ankylosaurs fairly rare. Sites with sample sizes over eight specimens begin to have equal likelihood of having any dinosaur group or mammals.

Figure 20 presents a similar distribution for non-dinosaurian groups. Only the turtle, crocodilian, and sphenodontian/lacertilian groups occur at single-specimen localities, and these groups occur throughout the sample-size distribution. Five of the six groups have appeared by the time sample sizes reach just three specimens (crocodilians, turtles, and sphenodontian/lactertilia from before and new groups pterosaurs, *Cteniogenys*, and Actinopterygii/*Ceratodus*). Frogs only occur at relatively large sample sizes.

Diversity and Sample Size

Scatter plots of the number of identified taxa by number of specimens for a sample of quarries were made in relation to each quarry's inferred paleoenvironment (Fig. 21) and stratigraphic level (Fig. 22). This was done to determine if for any given sample size (different sized quarries) diversity was related to either the environment or stratigraphic level. Rather striking differences in diversity are apparent in samples with relatively similar sizes, but none of these appear to be strongly correlated with either paleoenvironment or stratigraphic level. This would seem to suggest fairly even distribution of paleocommunity diversity across environments and through time and to suggest that taphonomic processes had only a minor effect on the overall apparent diversity of the formation.

Quarry Characteristics

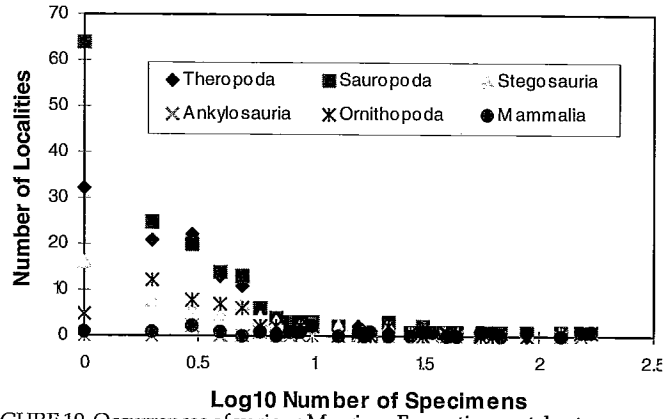

FIGURE 19. Occurrences of various Morrison Formation vertebrate groups at different sized quarries. X axis shows sample sizes of quarries; Y axis shows number of localities of each sample size containing respective vertebrate groups.

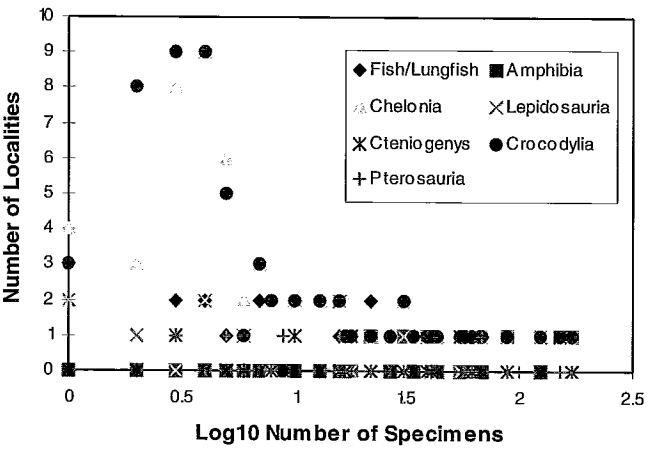

FIGURE 20. Occurrences of various non-dinosaurian Morrison Formation vertebrate groups at different sized quarries. X axis shows sample sizes of quarries; Y axis shows number of localities of each sample size containing respective vertebrate groups.

The percentages of quarries in different paleoenvironments are shown in Figure 23. Nearly three-quarters of the localities in the formation are in either fluvial channels or light gray-green, drab mudstone deposits representing poorly-drained floodplains. Quarries in other environments are more rare, but some of these produce large, diverse collections. A pie chart of the percentages of quarries in different stratigraphic levels (Fig. 24) shows a more even distribution, although more than half of the quarries are in Zones 4 and 5. (Engelmann and Fiorillo [2000] noted that although most major quarries are in the Brushy Basin Member or its equivalent level, nearly as many surface sites are found also in the underlying Salt Wash Member.) The effect on diversities of the large number of sites in channel and poorly-drained floodplain environments can be seen in Figure 25, which plots the number of taxa known from each paleoenvironment together with the number of quarries from each. Type 1 and Type 2 Ponds (and to some degree Type 2 Poorly-drained Floodplains) show significantly greater diversities relative to the number of sites than other paleoenvironments. This is mainly due to their preservation of large microvertebrate samples; Engelmann and Fiorillo (2000) also noted the association of microvertebrates with mudstones. Diversities in Channel and Type 1 Poorly-drained Floodplain environments seem to be largely a result of the large numbers of quarries in each.

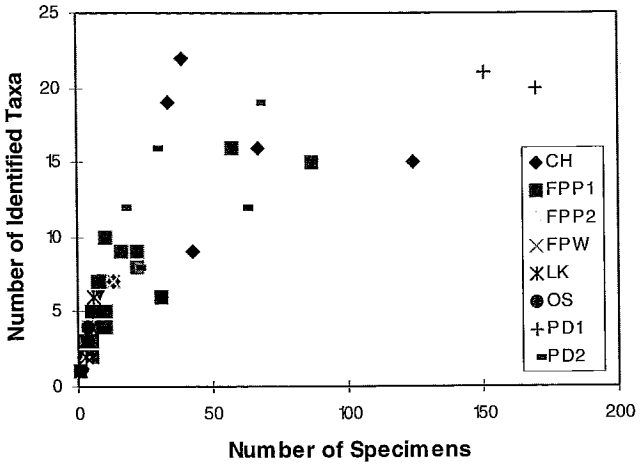

FIGURE 21. Distribution of diversity and sample size of Morrison Formation quarries in various inferred paleoenvironments. Paleoenvironmental abbreviations in legend as in Table 2.

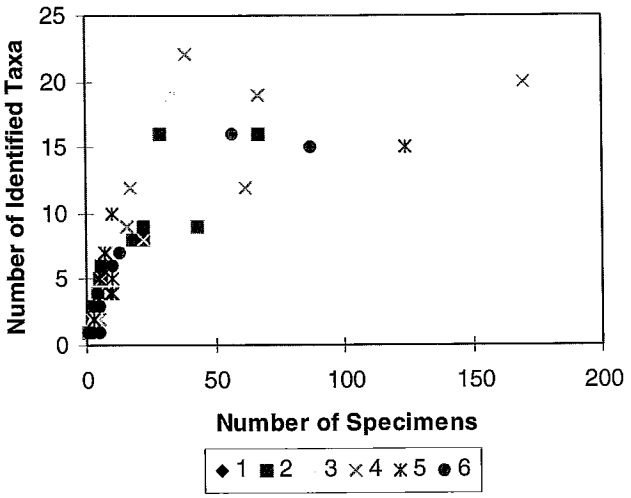

FIGURE 22. Distribution of diversity and sample size of Morrison Formation quarries from the six stratigraphic zones (legend indicates symbols for Zones 1–6). Paleoenvironmental abbreviations in legend as in Table 2.

Paleoecology

Abundance and Diversity of Groups

The abundance distribution of vertebrates in the Morrison Formation (as measured by number of localities at which they occur) shows groups of relatively common dinosaurs and a number of less common non-dinosaurian groups (Fig. 26). Only turtles and crocodilians are more common than several groups of dinosaurs. The Diplodocidae are the most common mainly because a number of genera are grouped here. *Allosaurus* and *Camarasaurus* are the most common genera, and *Stegosaurus* is next most common. This is a similar distribution to what Dodson et al. (1980) found except that they had *Diplodocus* and *Apatosaurus* separated out and between *Stegosaurus* and *Allosaurus/Camarasaurus* (which were equal in their counts). This would probably be the case if *Apatosaurus* and *Diplodocus* were separated out in this study as well. Interestingly, after turtles and semiaquatic crocodilians, sphenodontians and actinopterygian fish are the most common non-dinosaurian vertebrates. One of the rarer types of dinosaurs

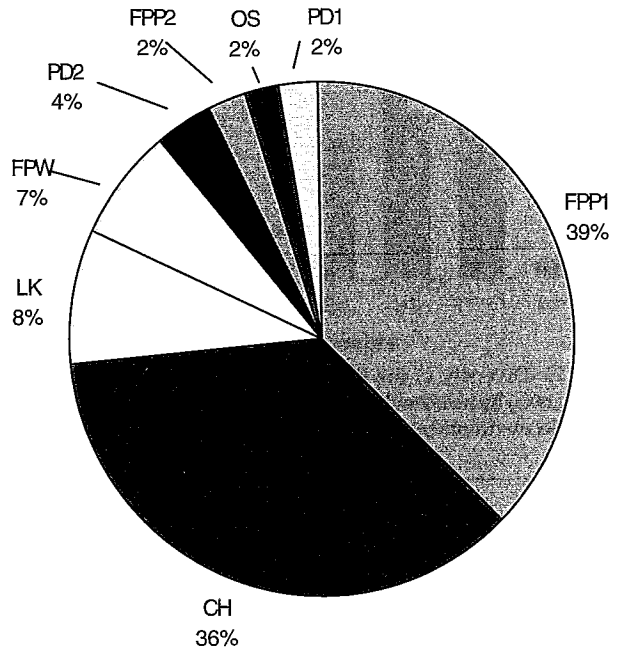

FIGURE 23. Percentage of Morrison Formation quarries in each of the paleoenvironments. Paleoenvironmental abbreviations as in Table 2.

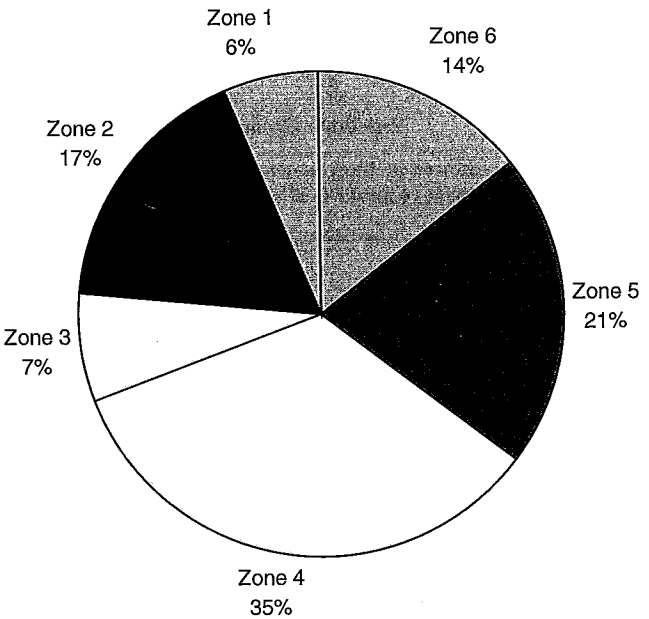

FIGURE 24. Percentage of Morrison Formation quarries in each of the stratigraphic zones.

are the ankylosaurs, which occur at fewer sites than dryolestid mammals. *Docodon*, which is often the most common single mammalian genus at any one locality at which it is found, is one of the rarest vertebrates in terms of number of localities. Multituberculates are present at 11 localities, whereas dryolestids occur at nine different sites but are represented by 173 specimens (an average of 19.2 specimens/site).

The number of taxa within different vertebrate groups in the Morrison Formation indicate that the greatest diversities occurred among the mammals, not surprisingly (Fig. 27). Sauropod

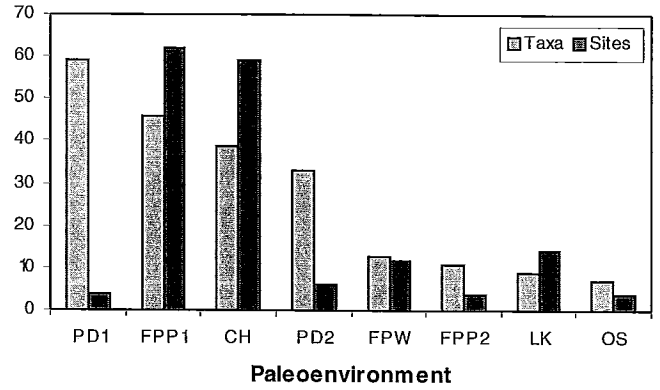

FIGURE 25. Diversity of the Morrison Formation vertebrate fauna (in number of taxa) by paleoenvironment compared to the number of quarries in each paleoenvironment. Paleoenvironmental abbreviations as in Table 2.

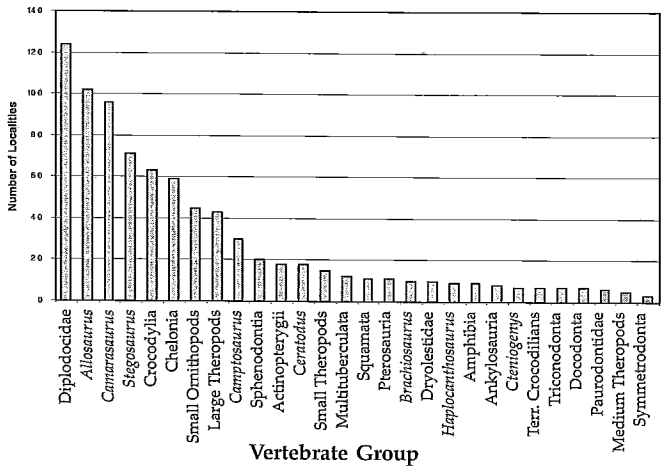

FIGURE 26. Abundances of Morrison Formation vertebrate groups, measured by the number of localities at which each occurs.

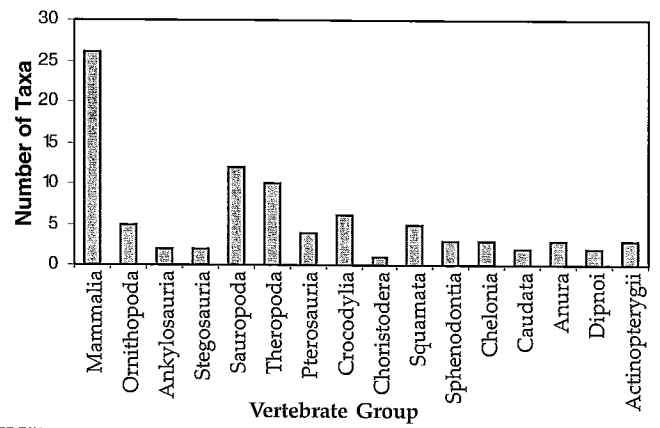

FIGURE 27. Diversities of major Morrison Formation vertebrate groups.

and theropod dinosaurs were the next most diverse, with about half as many identified taxa. The number of taxa represented by the mammals was probably even higher, as the analysis was done at the generic level, and several mammalian genera in the formation appear to have more than one valid species. The number of species within sauropod and theropod groups is not as likely to be underestimated to the same degree by the generic level analysis. The validities of different named species in these dinosaur groups are questionable. After the theropods and sauropods, the next most diverse groups of vertebrates are crocodilians, lizards, ornithopod dinosaurs, and pterosaurs.

The difference in diversity between mammals and other microvertebrates such as frogs and salamanders may suggest a real trend in the Morrison paleocommunity. Frogs, salamanders, and lizards all occur together with mammals in the large sample from Quarry 9, but there are still only two kinds of each of these animals known from the deposit as compared to more than 20 genera of mammals. Some lizards (and mammals) may have been arboreal and thus perhaps more likely to have their skeletons destroyed before burial than more ground-dwelling species of mammals, but frogs and salamanders should have had similar chances at preservation compared to mammals. Janzen (1976) suggested that modern small reptilian biomass and density in Africa were less than in the neotropics because of large herbivorous mammals. Habitat modification by the herbivores was one suggested possible cause of the low biomass, and the other was the increased diversity of carnivorous animals that mainly fed on the mammalian herbivores but which also occasionally fed on reptiles. Undoubtedly, in the Morrison Formation, sauropods had significant impact on the habitat and may have had some effect on reptilian density and perhaps diversity, if indeed that is one of the causes for the apparent lower modern reptilian densities and if a similar mechanism would have worked in the Jurassic. The modification caused by the very large sauropods would have been even greater than that caused today by elephants in Africa in which, in severe cases, large areas of woodland can be stripped nearly clean of vegetation (Owen-Smith, 1988). Another possible cause for the Morrison paleocommunity distribution would parallel the increased-carnivore hypothesis. The relatively high diversity of sauropods may have helped allow an increase in theropod diversity, and this may have resulted in greater predation on (and thus lower densities and perhaps diversities of) smaller reptiles.

Several of the Morrison theropods were fairly small and probably fed on smaller non-dinosaurian vertebrates as adults, but juveniles of larger theropod genera likely competed with the smaller species for these smaller items. A very young *Allosaurus*, for example, was about the size of adults of theropods such as *Coelurus* and *Ornitholestes*, and probably fed on some of the same animals (assuming that *Allosaurus* was not a social animal and that juveniles mainly hunted on their own and did not often feed on large verebrate carcasses brought down by adults, as young lions do). If this were the case, the rather great abundance and diversity of sauropods would have indirectly had an effect on small reptilian densities by allowing greater diversities and densities of theropod predators and thus greater predation intensities on small reptiles by small theropods.

The Upper Cretaceous Djadochta Formation of China represents an admittedly different paleoenvironment from that of the Morrison Formation, but it contains a paleofauna with an ankylosaur, a sauropod, a hadrosaur, and the ceratopsian *Protoceratops*, as well as the theropods *Oviraptor* and *Velociraptor*. Preserved with these dinosaurian taxa are 15 genera of lizards (Gao and Hou, 1995), a fact that may indicate that a less diverse and smaller large herbivore assemblage indeed allows for a more diverse and abundant community of small reptiles. This assumes, of course, that the differences between the Morrison and Djadochta faunas are not simply results of abiotic conditions.

It is difficult to determine whether habitat modification by sauropods or predation by theropods, or either, had any real influence on the relatively low diversity and abundance of small reptiles in the Morrison Formation. If either of these factors did have an influence it would at first seem that they should have had an equal effect on mammalian species, but this does not seem to be the case, at least with diversity, as there are about six times as many genera of mammals in the Morrison as there are of liz-

ards. This may be a result of different metabolisms and reproductive outputs in the two groups, however. Mammalian species may have been able to maintain much lower population densities than poikilotherms by having higher rates of production. Lower densities would have allowed greater diversities than would have been possible for the reptiles, and this may be why the number of mammalian genera is so much higher among microvertebrates.

The reasonably high diversity of vertebrates within the Morrison Formation may also indicate a moderately high degree of habitat and productivity heterogeneity, as areas with more consistent productivity tend to have lower diversities (Rosenzweig, 1995). For example, an increase in productivity in a desert environment, changing it to a semi-arid grassland, could decrease the original small vertebrate diversity by evening out the geographic habitat distribution. Even if one could correct for taphonomic biases against preservation in arid environments, the vertebrate paleofauna of the sand dune and interdune paleoenvironments of the Navajo Sandstone of the Early Jurassic, for example, probably was far less diverse than that in the Morrison Formation because productivity was low and fairly homogeneous in the Navajo. Higher productivity and habitat heterogeneity in the Morrison may have allowed the greater diversity.

Another possible, and somewhat alternative, determining factor in the Morrison Formation vertebrate diversity distribution is the diversity the paleocommunity "inherited" to begin with. In modern ecosystems, it appears that more varied habitats can allow more species, but that origination and extinction processes can produce many (or fewer) species and "force" life to recognize more (or fewer) niche habitats (Rosenzweig, 1995). The number of species or habitats can cause an increase in either, but a similar environment on an island can apparently contain fewer used habitats simply because there are fewer species than on the mainland. Thus, the relatively high diversity of some Morrison Formation vertebrate groups, or of the groups from the formation as a whole, may be a result of diverse groups already having been in the region, and given the same environment but a less diverse group of animals from the beginning, it would appear that there were fewer usable habitats. Therefore, diversity differences between groups within the Morrison Formation may alternatively be a result of past origination and extinction processes and not necessarily caused by specifics of the environment.

Diversity and Mass Distributions of Guilds

The diversity and mass distribution of Morrison vertebrate guilds are addressed graphically in Figures 28-30. Figure 28 shows the number of taxa in each of the five Locomotion/Habitat categories used in this study. The Terrestrial and Specialized Terrestrial categories are by far the most diverse, largely because of the mammals within the Specialized Terrestrial category. Dinosaurs and terrestrial crocodilians are the only animals in the Terrestrial category, but the large number of dinosaur taxa is mainly responsible for this category's high diversity. The low diversities among the pterosaurs in the Aerial category and among Semiaquatic and Aquatic animals may be caused by the more limited number of possible ecological niches in the more specialized locomotion modes and in the possibly more ecologically fine-grained nature of some of the aquatic habitats. On the other hand, the low aquatic diversity may be a result of the fact that many of the ponds within the Morrison apparently were ephemeral.

A graph of the diversities of the nine Feeding Mode guilds used in this study (Fig. 29) indicates some inverse correlation between body size and diversity within certain larger guilds. Among Herbivorous dinosaurs, for example, Low Browsers, which include relatively small dinosaurs such as ornithopods, are the most diverse guild; Medium and High Browsers, both including only

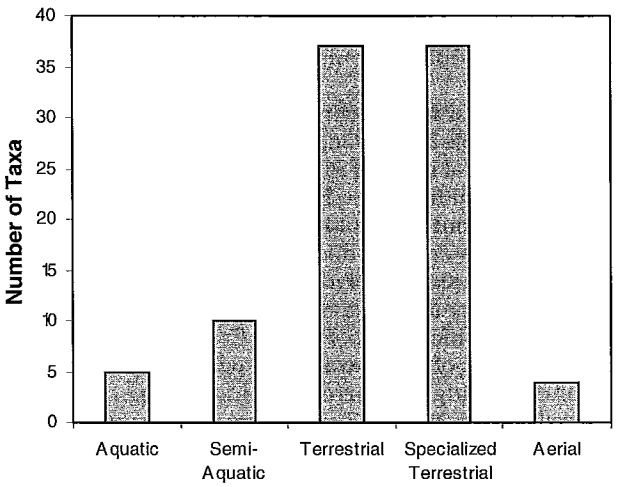

FIGURE 28. Diversities of Morrison Formation vertebrate Locomotion/Habitat guilds.

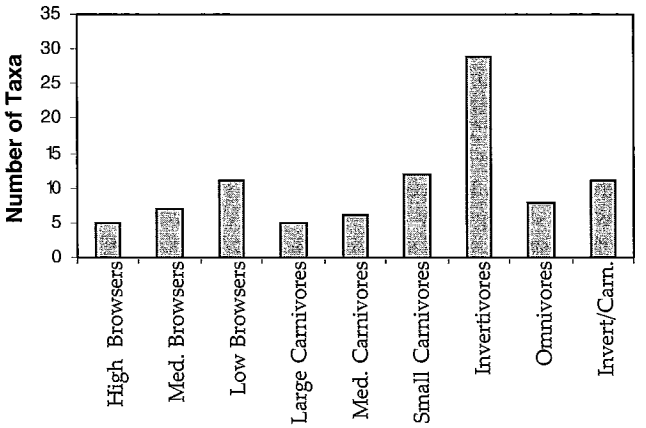

FIGURE 29. Diversities of Morrison Formation vertebrate Feeding Mode guilds.

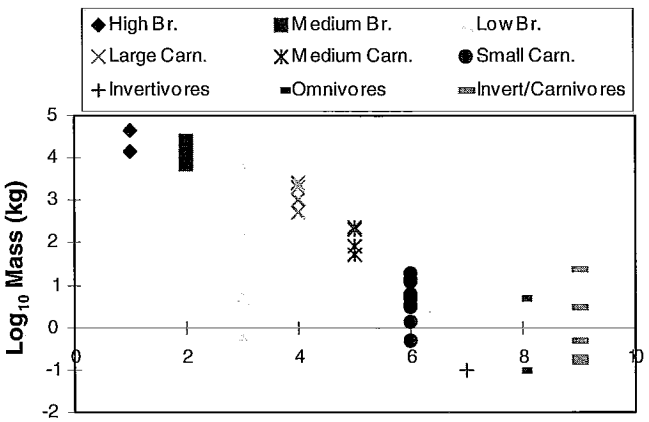

FIGURE 30. Estimated mass distributions for Morrison Formation vertebrate taxa in each Feeding Mode guild.

sauropods, are progressively less diverse. The Small Carnivore guild also contains about twice as many genera as the Medium and Large Carnivores. The Invertivores are all less than 1 kg in weight and are far more diverse than any other guild. This guild is composed mainly of mammals and lizards and a few other groups. That diversity is highest for the smaller animals, particularly the Invertivores, should not be surprising because these taxa

would see most environments as ecologically coarse-grained and would be able to develop relatively more specialized ecological niches than would larger animals such as sauropods, to which the Morrison floodplain would have seemed relatively fine-grained.

The masses of taxa within the nine Feeding Mode guilds (Fig. 30) demonstrate a wide range of sizes for Low Browsers and Carnivores. The total range of masses for all vertebrates is nearly six orders of magnitude; Low Browsers range over about four and Carnivores about three and a half. The smallest animals include Invertivores and the docodonts and multituberculates among the Omnivores; Invertivore/Carnivores include a range of taxonomic groups and thus have a wide mass range.

The range of Morrison Formation Carnivore sizes probably reflects their range of prey taxa, the progressively larger carnivores concentrating on correspondingly larger prey. Van Valkenburgh and Molnar (2002) noted a greater separation in body size among sympatric theropods than is seen in mammalian predator faunas, and this may relate in part to the range of prey sizes. The largest Morrison Formation Carnivore is significantly smaller than several of the herbivorous dinosaur species of the time, and among the most common Herbivores and Carnivores, *Stegosaurus* (~5000 kg) weighs about five times as much as *Allosaurus* (~1000 kg), and *Diplodocus*, one of the lighter sauropod taxa (~12,500 kg), is more than an order of magnitude heavier. *Allosaurus* was the largest common theropod of the time, as *Torvosaurus* (~1950 kg) is rare, and *Saurophaganax* (2720 kg) is known from just one locality. *Allosaurus* specimens outnumber all other theropod specimens nearly 2 to 1 in the Morrison, so this genus was ecologically very important (Foster and Chure, 1998), but based on its small size relative to some of the available herbivorous dinosaur species, it probably did not feed often on adult sauropods except as carrion. Adult lions feed mainly on animals about four times smaller to just larger than themselves but may attack and feed on animals up to four times larger (Kingdon, 1997). Admittedly, there are major functional morphologic, systematic, and physiologic differences between *Allosaurus fragilis* and *Panthera leo*, but as an efficient, large predator, the lion serves as a sufficient modern analog, and there seems little reason to suspect that adult *Allosaurus* would have had any success attacking healthy adult sauropods weighing at least ten times as much.

One related issue is whether *Allosaurus* would have been mainly a lone or small-pack hunter. Even if it were a pack hunter, it is still likely that adult *Allosaurus* concentrated more on juvenile sauropods, adult ornithopods, and perhaps stegosaurs than on adult sauropods. Pack-hunting wild dogs rarely attack animals more than twice their body size (Kingdon, 1997), and similarly, a 1000 kg *Allosaurus* probably preyed on animals such as those listed above that were its size or slightly larger and would have been less likely to attack a 24 tonne adult *Apatosaurus*, for example. Van Valkenburgh and Molnar (2002) suggested that large theropods likely hunted animals as large or somewhat larger than themselves and that carcass theft may have been a common tactic as well. In any case, the distribution of body masses in the Morrison Formation Feeding Mode guilds is very wide and quite different from anything seen today.

The diversities within weight categories for predator and prey groups (Fig. 31) show an interesting pattern. For this graph, only terrestrial taxa were considered, including theropods, terrestrial crocodilians (e.g. "*Fruitachampsa*"), and the unnamed snake among predators and sauropods, ornithopods, ankylosaurs, stegosaurs, lizards, sphenodontians, and mammals among prey. Taxa were counted at the generic level except in the case of the mammals, which were counted by group (e.g. triconodonts) only so that, given the tremendous mammalian diversity, the graph would be more readable on a non-log scale.

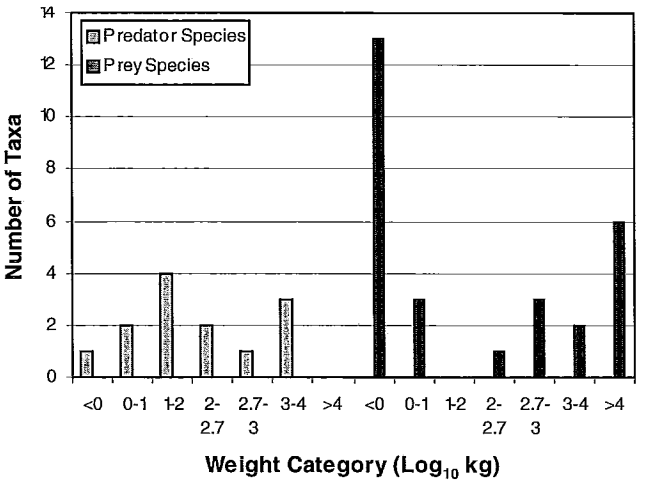

FIGURE 31. Diversities of weight categories for Morrison Formation terrestrial vertebrate taxa. Predator and prey species compared. Note bimodal distribution of prey species with low diversity in low-middle size ranges and peak predator diversities at correspondingly low prey diversities.

The weight class distribution of prey taxa in Figure 31 is similar to that seen by Wing and Tiffney (1987) for herbivores in the Morrison Formation, with many small and very large taxa and few in the middle size classes. This pattern is also seen in the Lower Cretaceous Wealden and to some degree in the Upper Cretaceous Judith River Formation (Wing and Tiffney, 1987). In the Morrison Formation, there is no such bimodality to the weight distributions of predator taxa, and the predatory animals are more evenly distributed across the weight categories (Fig. 31). There is actually a greater diversity of predator taxa in the middle weight categories where there are almost no prey taxa. In fact, the peak predator diversities occur in size classes (10–100 kg; 1–10 tonnes) just larger than some of the peaks for prey taxa (<10 kg; 500–1000 kg). The predators in each of the peak size classes, as well as those just smaller, probably fed mainly on the prey groups just smaller than them. Thus, the small theropods in the 10–100 kg category (*Coelurus, Ornitholestes*, etc.) probably fed mainly on the prey taxa forming the <1 kg and 1–10 kg peak categories (lizards, sphenodontians, mammals, small ornithopods). Also, the large theropods in the 1–10 tonne category probably fed on the prey taxa in the 100–500 kg, 500–1000 kg, and 1–10 tonne categories (*Camptosaurus, Dryosaurus*, stegosaurs etc.).

It is likely that the adult sauropods in the 10–100 tonne size class were, in most cases, safe from predation, and because this largest size class is second in diversity only to the <1 kg class, I would suggest that the very low diversity among prey taxa in the 10–500 kg size range is at least partly because of the great diversity of dinosaurs with much larger adult sizes. Juvenile sauropods, stegosaurs, and ankylosaurs probably would have initially occupied the 10–500 kg range and would have provided food for large theropods and heavy competition for any herbivorous taxa with 10–500 kg adult sizes. Prey taxa less than 10 kg may have been less affected by competition from juveniles of the larger dinosaur taxa.

Stucky (1990) suggested that one possible reason for the size dichotomy seen in Late Cretaceous vertebrate communities was that habitat modification by large herbivores increased the visual hunting capabilities of predators by opening up the understory. Thus, there would have been selective pressure limiting the size of the animals living on the forest floor. This same pro-

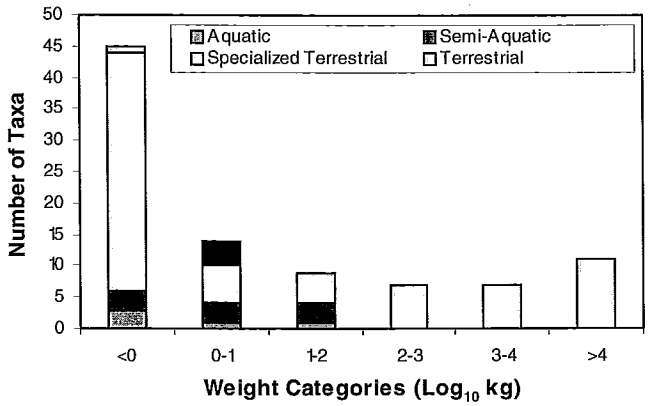

FIGURE 32. Diversities of Morrison Formation vertebrate weight categories and composition of each by taxa in respective Locomotion/Habitat guilds.

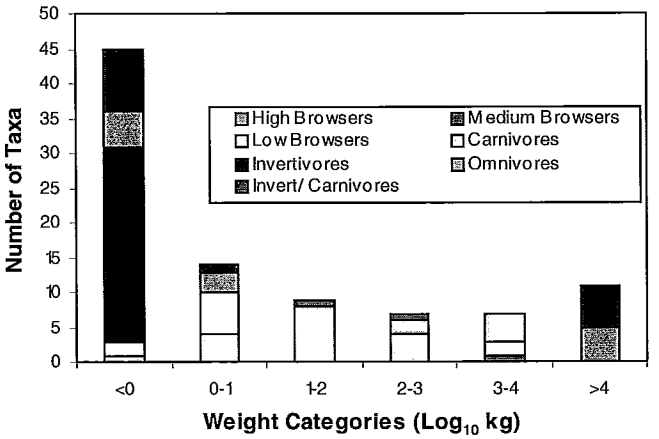

FIGURE 33. Diversities of Morrison Formation vertebrate weight categories and composition of each by taxa in respective Feeding Mode guilds.

cess may have been operating during the Late Jurassic as well. Browsing by the large herbivores of the time could have limited the understory and put pressure on prey taxa to develop either small adult sizes or, in the case of sauropods, very large adult sizes in order to avoid predation. If the 10–500 kg size range was a dangerous one in the Morrison Formation environment, then the prey animals may have stayed mostly below it or occupied it only temporarily as juveniles. The predator diversity peak in the 10–100 kg indicates that certainly the <10 kg prey taxa were not entirely safe, but taxa in the 10–500 kg range would have been potential prey for nearly all the predators of the time, from the 10–100 kg small theropods and medium-sized theropods like *Marshosaurus* up to the large and common 1 tonne *Allosaurus*. With predators ranging all sizes and vegetative cover relatively restricted by browsing, prey taxa may have adopted the strategy of either staying small or becoming very large in order to limit their number of potential predators.

The diversity in different size classes and the number of taxa in each Locomotion/Habitat category are shown in Figure 32. The overall distribution of diversity in size categories is vaguely similar to the modern Serengeti ecosystem and different from tropical ones (Damuth et al., 1992) in that the smallest size class is the most diverse, but the largest size class is actually more diverse than some of the intermediate classes. The smallest size class (<1 kg) contains about three times as many taxa as the next most diverse class. Diversity of Terrestrial vertebrates is fairly even across all size classes down to 1 kg; no Aquatic or Semiaquatic taxa are larger than the 10–100 kg category; and all Specialized Terrestrial animals are small (<1 kg). If finer measurement of the masses of very small animals were possible for the Morrison taxa, the modal size class would likely be just heavier than the smallest size class, unlike what is seen at this resolution (Brown, 1995).

The diversity distributions of Feeding Mode guilds are a little more complex (Fig. 33). Invertivore/Carnivores are most diverse at the smallest body sizes but range up to 100–1000 kg; Omnivore diversities are about equal among the <1 kg and 1–10 kg categories and consist of multituberculate/docodont and turtle assemblages, respectively. Invertivores occur only in the <1 kg category; Carnivores occur in all weight categories up to 10,000 kg but are most diverse in the 10–100 kg category; and interestingly, no Low Browser taxa are between 10–100 kg. The pattern seen here is similar to that noted by Wing and Tiffney (1987) for the middle Cretaceous in that the diversity of small herbivores (Low Browsers <100 kg) is fairly low. They attribute this to a pattern of generalized herbivory before the Campanian.

Biomass vs. Numerical Abundance

One interesting feature of the Morrison Formation vertbrate paleocommunity is that there are major differences in the abundances of different guilds and ecological categories depending on whether the abundances are measured by the corrected percent biomass or by the corrected percent of individuals. Among the Locomotion/Habitat categories, for example (Fig. 34), Terrestrial taxa are the second least abundant animals in terms of numbers but they account for over 95% of the biomass. For the Feeding Modes, the small Invertivores, along with Omnivores and Invertivore/Carnivores dominate in terms of numbers, but Low, Medium, and High Browsers comprise close to 90% of the biomass (Fig. 35). This is not unexpected, as in modern megaherbivore communities, elephants and other large herbivorous mammals are outnumbered numerically but dominate in terms of biomass. Populations of white rhinoceros, black rhinoceros, and giraffe in the Umfolozi Game Reserve in southern Africa account for only 7.5% of the herbivorous animals in the region but for 50.3% of the biomass density (Owen-Smith, 1988). Given the significantly greater individual biomasses of the large herbivores in the Morrison Formation, the more extreme differences in abundance and biomass seen in Figures 34 and 35 are not surprising, and the effects on the habitat and other species probably were more pronounced but not necessarily that different from what is seen today in megaherbivore communities. Elephants, for example, have a large impact on vegetation, but the effects in many cases are positive for some smaller herbivorous species. The replacement of woodlands by rapidly growing shrubs after very large herbivores have passed through an area can be advantageous to smaller, browsing herbivorous animals (Owen-Smith, 1988).

General Diversity Trends

Rarefaction—One problem of diversity comparisons is the different number of specimens in each sample. One sample may contain more species than another but it may also contain more specimens. What would be the number of species in this larger sample if it had the same number of specimens as the other sample? If one could determine this, different-sized samples could be directly compared to see if the samples came from similarly diverse original communities. Sanders (1968) described a method for determining this expected diversity for "rarefied" samples. This method can slightly overestimate the expected number of taxa (Gotelli and Graves, 1996; Hayek and Buzas, 1997), so the

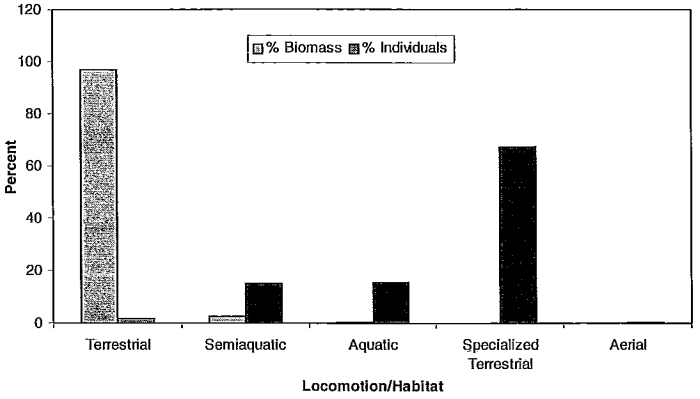

FIGURE 34. Comparison of corrected percent individuals and corrected percent biomass of Morrison Formation vertebrates by Locomotion/Habitat guilds.

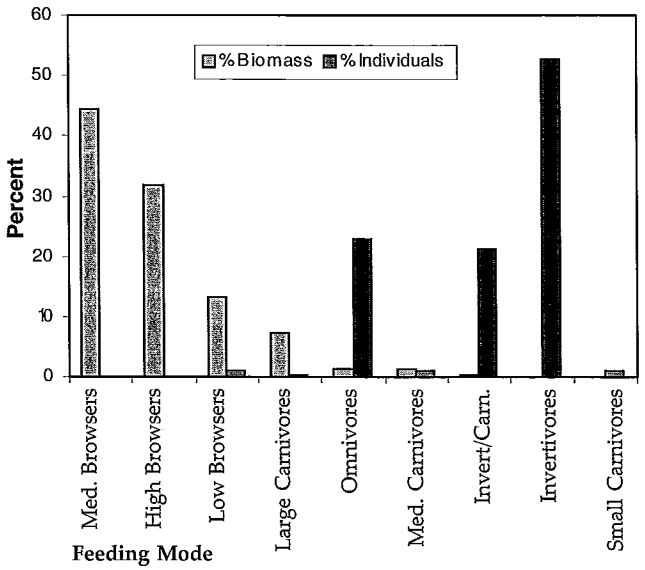

FIGURE 35. Comparison of corrected percent biomass and corrected percent individuals of Morrison Formation vertebrate taxa by Feeding Mode guilds.

method of Tipper (1979) was used for this study. Gotelli and Graves (1996) cover some of the assumptions involved in rarefaction models.

The scatter plot distribution of expected numbers of taxa at different, rarefied sample sizes for each Morrison stratigraphic level above Zone 1 (Fig. 36) suggests that the diversity of all vertebrate taxa in the formation was consistent throughout the time of deposition. These data are presented as a general indication of the comparative diversity of the different levels within the Morrison Formation. The 95% confidence intervals for the stratigraphic levels seem to overlap at most comparable sample sizes.

Simpson Index—Another method of comparing diversity from different sample sizes was developed by E. H. Simpson (1949), who proposed an index based on the numbers of specimens of each species (n) and the total sample size (N). The Simpson Index (SI) ranges between 1 and 0. The SI value grows as diversity declines; thus an SI value of 1 is the upper limit, at which all individuals in the sample belong to one species. The SI value for the Morrison Formation as a whole is 0.060. The SI values for

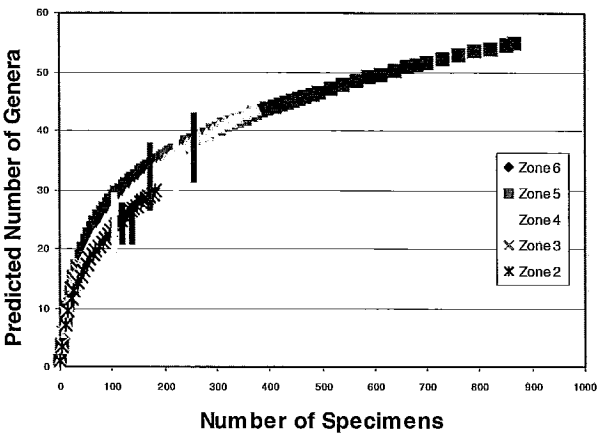

FIGURE 36. Rarefaction curves comparing expected diversities at smaller sizes for the samples from stratigraphic Zones 2–6. Bars indicated 95% confidence intervals. The curves suggest that overall diversity of the Morrison Formation vertebrate fauna was at similar levels throughout the time of deposition.

TABLE 6. Calculated Simpson Index (SI) for the Morrison Formation.

Simpson Index for the Morrison Formation overall:	0.060
Simpson Index for Morrison Formation Stratigraphic Levels:	
Zone 6	0.072
Zone 5	0.081
Zone 4	0.090
Zone 3	0.065
Zone 2	0.070
Zone 1	—

$SI = \Sigma((n^2-n) / (N^2-N))$

stratigraphic levels in the Morrison range from 0.065 to 0.090 (Table 6) and suggest a relatively consistent and diverse community from each level. Though all the levels have very close SI values and the differences may be insignificant, it is interesting that Zone 4, which contains the Fruita Paleontological Area and its microvertebrate assemblage, apparently has the relatively lowest diversity. On the other hand, it is also interesting that Zone 5, with Quarry 9, is not the relatively most diverse. The Morrison Formation probably had a consistent, relatively high level of vertebrate diversity throughout its time of deposition and, despite large, diverse single quarries in only some levels, the SI value appears to show this.

Guild Diversity Trends

The diversities of Locomotion/Habitat categories through the six stratigraphic zones demonstrate relative consistency throughout most of the time of the Morrison (Fig. 37). The sample size of Zone 1 is too low to allow comparison, but above that it is apparent that Terrestrial and Specialized Terrestrial modes are most diverse, followed by Semiaquatic. Expected values are too low to permit X^2 tests on all Locomotion/Habitat modes and all stratigraphic levels, but analysis of the above three modes from Zone 4 up through Zone 6 indicates no significant change in diversity within the modes ($X^2 = 6.7$, critical value = 9.5, degrees of freedom = 4 at the 0.05 level). Based on the graph, however, it appears that the diversity of the Specialized Terrestrial mode has a lower than expected diversity in Zone 3. The analysis has to be restricted to the Terrestrial and Specialized Terrestrial modes in this case to maintain high enough expected values, but including

Zone 3 through Zone 6 demonstrates that the Specialized Terrestrial category is less diverse than expected ($X^2 = 10.1$, cv = 7.8, df = 3). Considering, however, that Zone 3 is the shortest and thinnest stratigraphic level and that there are few quarries in it (and thus few specimens and taxa), this low diversity is probably a product of sampling effects and not necessarily a real paleobiologic phenomenon. From the graph, then, it would appear that diversity within Locomotion/Habitat categories remained consistent relative to overall diversity through the time of Morrison Formation deposition.

The diversity of Feeding Mode guilds is also consistent throughout the time of the Morrison Formation (Fig. 38). Again, as with most analyses attempted here, the expected values are too low to allow comparison of all feeding guilds over all stratigraphic levels, but comparison of the Invertivore and Invertivore/Carnivore guilds between Zones 4 and 5 indicates that the diversity of the two remains consistent within expected levels ($X^2 = 1.2$, cv = 3.8, df = 1). A qualitative look at Figure 38 shows that the number of Feeding Mode guilds at all levels in the Morrison Formation remains relatively high, though the total numbers of taxa identified from each level vary. It is also interesting that the diversity of guilds seems to be relatively even within and between stratigraphic levels; no one guild seems to have particularly high or low diversity relative to any one level. This too seems to be characteristic of a number of modern communities. Gotelli and Graves (1996) reviewed some of the hypotheses regarding community "assembly rules," and several of the studies found relatively even guild frequencies and distributions. It seems to be fairly common for species communities to fill available guilds evenly in favor of unevenly. For example, a five-species community with three guilds would distribute the species (2/2/1) more often than (3/1/1). Various hypotheses exist for why this is true in modern assemblages, but in the case of the Morrison Formation it is interesting that the same pattern is apparent and that it is consistent at each level of the formation.

In Figure 39 diversities of theropods in the Morrison Formation were compared relative to overall dinosaur diversity using the six stratigraphic levels based on Turner and Peterson (1999). The relative diversities of theropod dinosaurs increase upward through the lower two-thirds of the formation. The second highest and highest levels, however, have the highest and lowest theropod diversity percentages, respectively, even though they have neither the highest nor lowest overall dinosaur diversities, indicating the possibility of a slight increase and then decrease in theropod diversity in the upper part of the Morrison. That the pattern may be real is indicated by the fact that the sample sizes from the upper two levels are each larger than at least one of the underlying, and more diverse, levels.

The theropod genus *Allosaurus* is the only theropod taxon to occur throughout the formation stratigraphically, and it is also, by far, the most geographically widespread (Foster and Chure, 1998; Chure et al., 2000). Within all stratigraphic levels and depositional environments, *Allosaurus* has a relative abundance of approximately 60–70% of all theropod specimens (Fig. 40). *Allosaurus* also constitutes approximately 13% of all dinosaur specimens, across all stratigraphic levels and depositional environments. These percentages have not been corrected for possible taphonomic bias against smaller-bodied animals, however, and smaller theropod species probably accounted for a larger percentage of the original theropod population than the current record suggests. However, among larger theropods *Allosaurus* was consistently dominant numerically through both time and space and must have been a very important ecological component of the Morrison dinosaur community.

The diversity distribution of body sizes in the Morrison

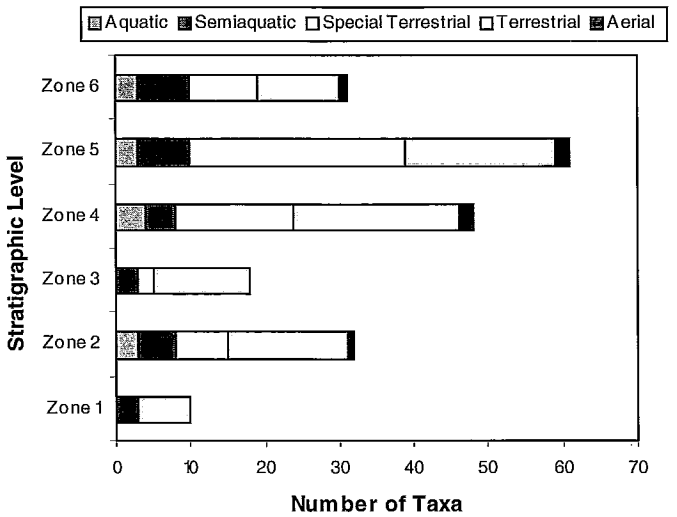

FIGURE 37. Diversities of Morrison Formation vertebrate Locomotion/Habitat guilds by stratigraphic level.

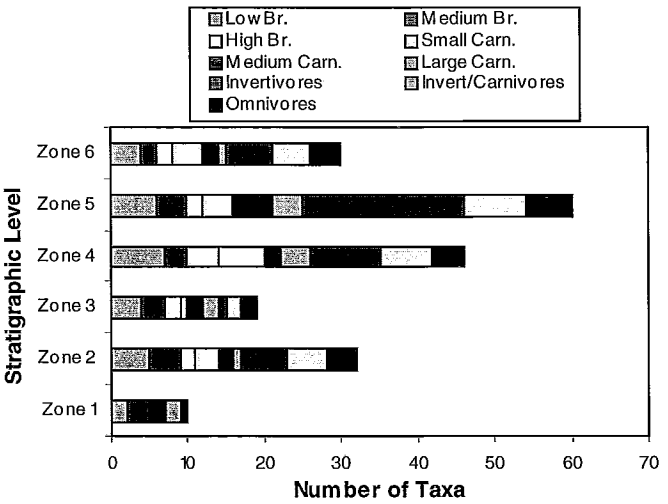

FIGURE 38. Diversities of Morrison Formation vertebrate Feeding Mode guilds by stratigraphic level.

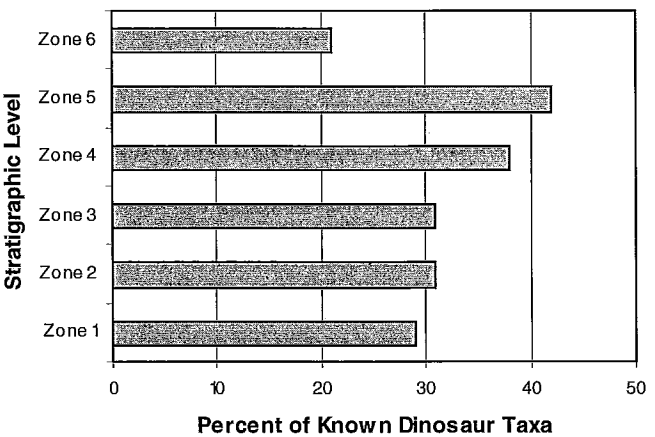

FIGURE 39. Diversity of theropods from each stratigraphic level in the Morrison Formation, as a percentage of the number of known dinosaur taxa from each level.

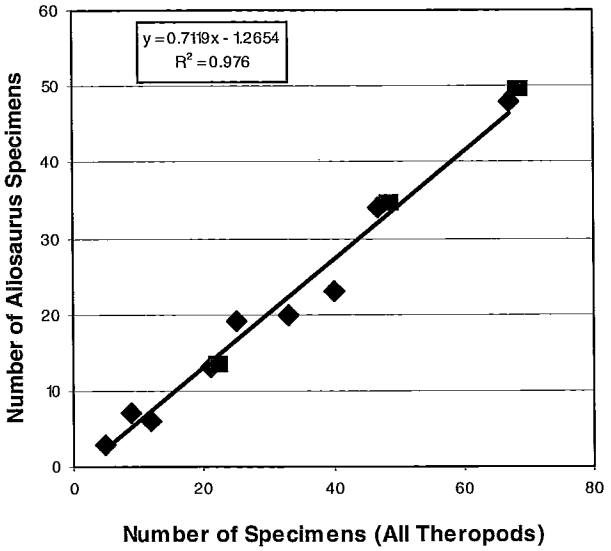

FIGURE 40. Number of *Allosaurus* specimens compared to total number of theropod specimens, showing the genus's consistency of relative abundance environmentally and temporally. Filled diamonds represent the samples from respective stratigraphic levels; boxes represent samples from separate paleoenvironments.

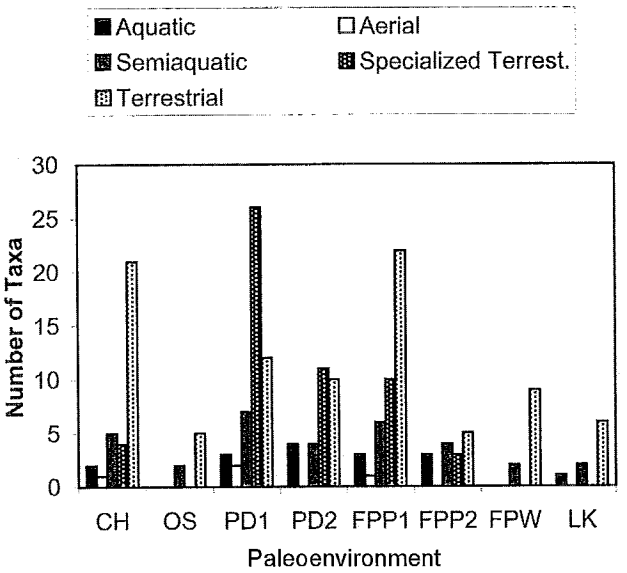

FIGURE 42. Diversities of Morrison Formation vertebrate Locomotion/Habitat guilds in each paleoenvironment. Paleoenvironmental abbreviations as in Table 2.

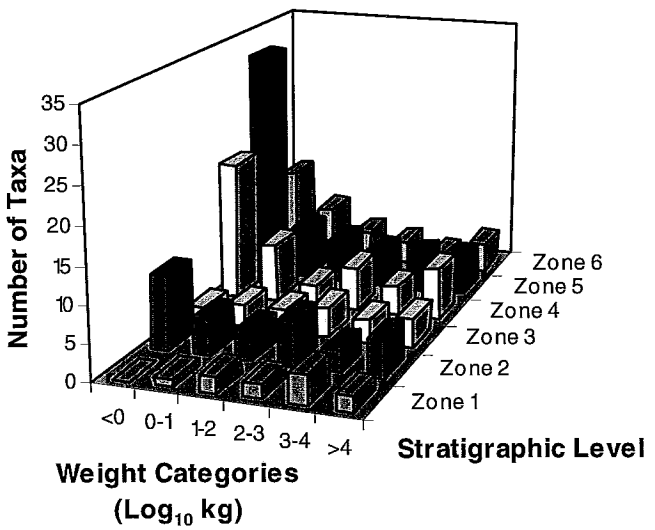

FIGURE 41. Diversities of Morrison Formation vertebrate weight categories by stratigraphic level.

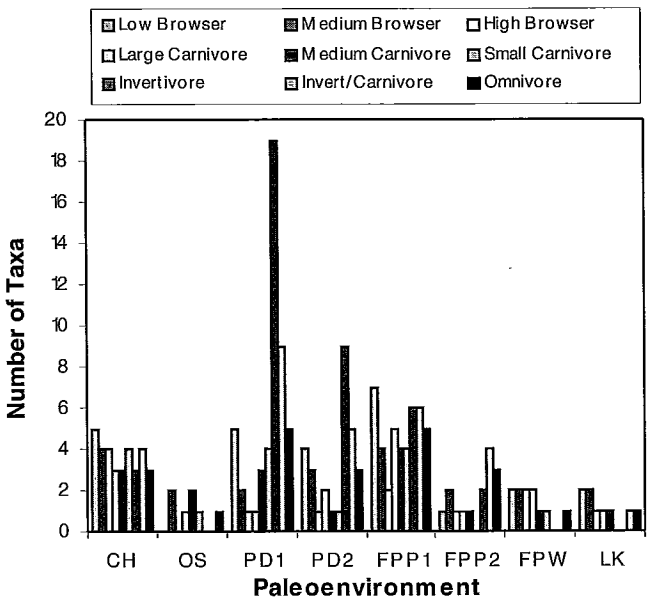

FIGURE 43. Diversities of Morrison Formation vertebrate Feeding Mode guilds in each paleoenvironment. Paleoenvironmental abbreviations as in Table 2.

Formation is similar to some modern environments (Fig. 41). Smaller-sized animals are more diverse, and this pattern holds for all stratigraphic levels for which it is possible to test. Above the 1–10 kg category the diversities differ, but often the >10,000 kg category is more diverse than the several smaller categories. The <1 kg and 1–10 kg categories were examined from Zone 4 to Zone 6, and the relative diversities were consistent ($X^2 = 2.7$, cv = 5.99, df = 2). Thus, there does not seem to be any significant change in diversities of size classes of vertebrates over time in the formation.

Overall diversities in different paleoenvironmental conditions (Figs. 42–43) are somewhat dependent on the sample sizes from the quarries. Paleoenvironments with few quarries and thus few specimens (Well Drained Floodplains, Lacustrine, and Overbank Sands) have low diversities. Channel sand deposits preserve a far greater diversities of Terrestrial animals; this is also largely true of Poorly Drained Floodplain deposits. Pond deposits preserved great diversities of Specialized Terrestrial animals; the high diversity of the Specialized Terrestrial mode in Type 1 Ponds is mostly due to the sample at Quarry 9. The diversity differences in different paleoenvironments for the Terrestrial and Specialized Terrestrial categories probably reflects Terrestrial animals' living across a range of environments, as Dodson et al. (1980) found for the sauropods, and the restriction of preservation of microvertebrates to certain taphonomic conditions in some paleoenviroments. The distributions of Feeding Mode guild diversities across most paleoenvironments is fairly even, particularly in channels (Fig. 43). Diversities of Invertivores and Invertivore/Carnivores in Pond and Type 2 Poorly Drained Floodplain environments are a bit higher than normal. Within the Pond

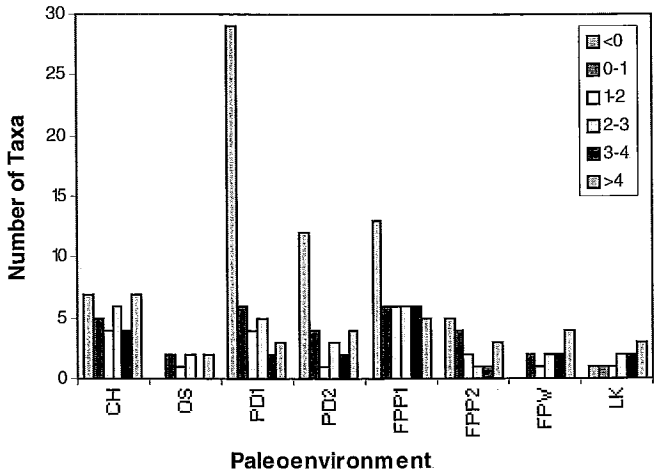

FIGURE 44. Diversities of Morrison Formation vertebrate weight categories in each paleoenvironment. Paleoenvironmental abbreviatons as in Table 2. Weight categories in legend are in Log10 kg.

deposits this is probably an effect of preservation, and much of the diversity in the Type 1 Pond deposits is a result of the Quarry 9 sample, which has many taxa of Invertivores that are only known from there.

The diversities of different size classes of vertebrates show relatively even distributions for some paleoenvironments as well (Fig. 44). Channel environments preserved fairly even diversities of taxa in all size classes, but Pond deposits and Type 1 Poorly Drained Floodplains preserve greater diversities of small taxa. Well Drained Floodplains are opposite in preserving mainly larger animals. The variation seen here is most likely taphonomic and not a result of differences in the communities from which the samples are drawn.

Paleobiogeography

Comparison of the diversities of the Feeding Mode guilds across the north-south and east-west geographic tiers (Figs. 45–46) demonstrates that the peak diversities in each tier occur in the Invertivore and Low Browser categories. The degree to which this trend is visible depends on the sample size from each tier; the Middle north-south tier and the Middle and West east-west tiers demonstrate the trend best. Overall known diversities in the North, South, and East tiers are low due to relatively low sample sizes, and these tiers still show signs of similarity to larger sample-sized tiers. No geographic trend in Feeding Mode guild diversity distribution is thus apparent.

The same consistency between tiers as seen above is apparent in the plots of diversities of weight categories (Figs. 47–48). Each tier shows, to some degree or another, a similar distribution to that of the whole formation (Fig. 32), where the <1 kg category is by far the most diverse, subsequently greater weight categories are progressively less diverse, and the >10,000 kg category increases slightly in number of taxa over the next smallest category or two. It would appear, then, that there is no major variation in the diversity of weight classes across geographic ranges in the Morrison Formation.

A similar homogeneity was found in the north-south distributions of individual dinosaur genera for the Morrison Formation (Foster, 2000), and although this pattern seems to be a general rule for most taxa in the formation, some individual microvertebrate taxa do demonstrate distributions that suggest some heterogeneous abundance zonation may have been present (Engelmann and Callison, 1998; Foster and Trujillo, 2000).

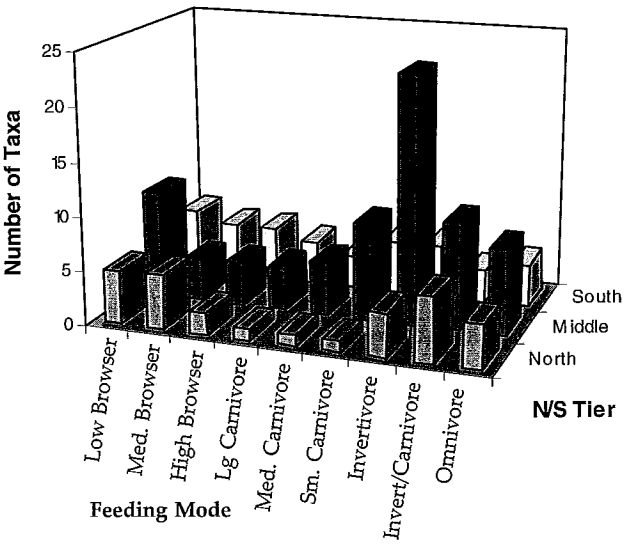

FIGURE 45. Diversities of Morrison Formation vertebrate Feeding Mode guilds by north-south geographic tier.

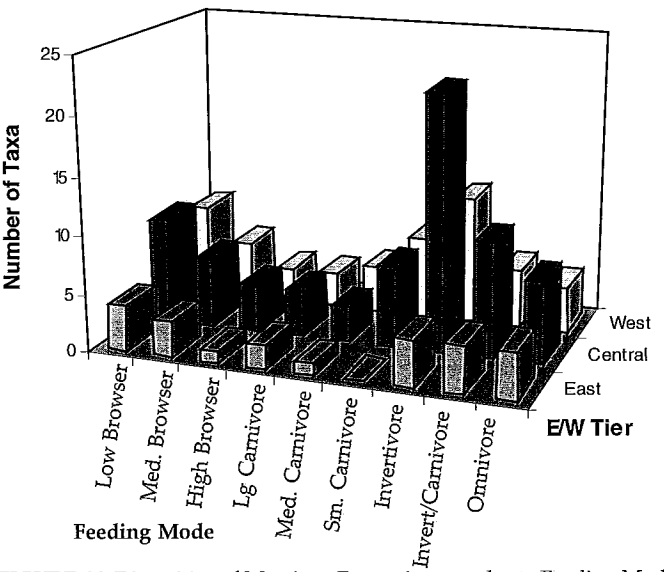

FIGURE 46. Diversities of Morrison Formation vertebrate Feeding Mode guilds by east-west geographic tier.

Relative Abundance Trends

The relative abundance (as measured by the corrected percentage of individuals) of the Locomotion/Habitat categories at different stratigraphic levels in the Morrison Formation (Fig. 49) shows relative stability over time. Where they are known, Specialized Terrestrial taxa dominate in terms of numbers and by a consistent amount, along with, to a lesser degree, Semiaquatic taxa. There seems to be a trend toward decreasing abundance of Terrestrial taxa upward through the formation (Zones 1 and 3 have too few specimens to consider in an analysis), but this may be a result of corresponding increases in sample sizes and thus diversities of smaller taxa. Analysis of the relative abundances of Specialized Terrestrial and Semiaquatic taxa from Zones 2, 4, 5, and 6, indicates that the percentage of Semiaquatic individuals in Zone 2 is significantly higher (30.6%) than expected (~18%) and that at other levels the percentages are within expected ranges (X^2 = 15.2, cv = 7.8, df = 3). The sample sizes of the four stratigraphic levels analysed range from 207 to 1425 specimens and

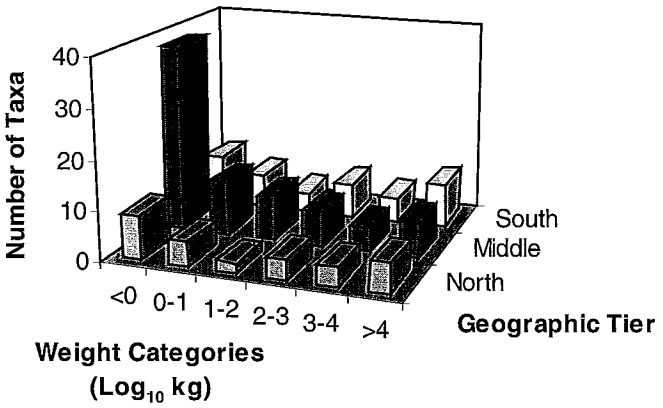

FIGURE 47. Diversities of Morrison Formation vertebrate weight categories by north-south geographic tier.

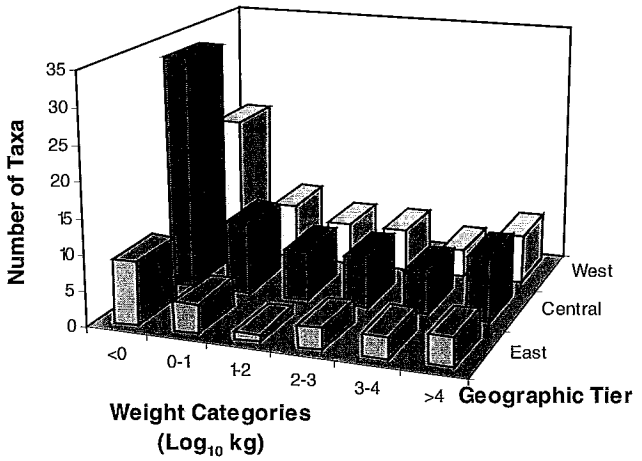

FIGURE 48. Diversities of Morrison Formation vertebrate weight categories by east-west geographic tier.

Zone 2 has 253 specimens, so the difference in percentage of Semiaquatic taxa at that level is not necessarily just because of very small sample size relative to other levels that are within the expected range. Still, what an apparently higher percentage of Semiaquatic taxa lower in the formation may mean is unclear. Unfortunately, expected values are too low to test whether the diversity of the Semiaquatic category is higher than expected as well in Zone 2.

The relative abundances of Feeding Mode guilds through the Morrison stratigraphic levels (Fig. 50) indicate that other than an apparent drop in abundance of Invertivore/Carnivores and corresponding increase in Invertivore abundance in Zone 6 (Invert/Carnivore expected % = ~15, observed = 5.4, X^2 = 27.4, cv = 12.6, df = 6), the pattern is relatively consistent through most levels. The pattern in Zone 6 may be a result of its having the fewest specimens of the levels compared, though at 207 specimens it is not particularly small.

The relative abundances of different weight classes by stratigraphic level (Fig. 51) are dominated by the <1 kg class and demonstrate no significant change from Zone 4 through Zone 6 (X^2 = 1.3, cv = 5.99, df = 2). However, the inclusion of Zones 3 and 2 (analyzing again only the <1 kg and 1–10 kg classes due to minimum expected values needed) changes the picture a bit. With Zones 2 through 4, there is a significant change in the relative abundances of the 1–10 kg classes between Zones 2 and 3 and Zones 5 and 6 (X^2 = 26.0, cv = 9.49, df = 4). Specifically, Zones 2 and 3 have higher than expected percentages of 1–10 kg taxa (21.6–

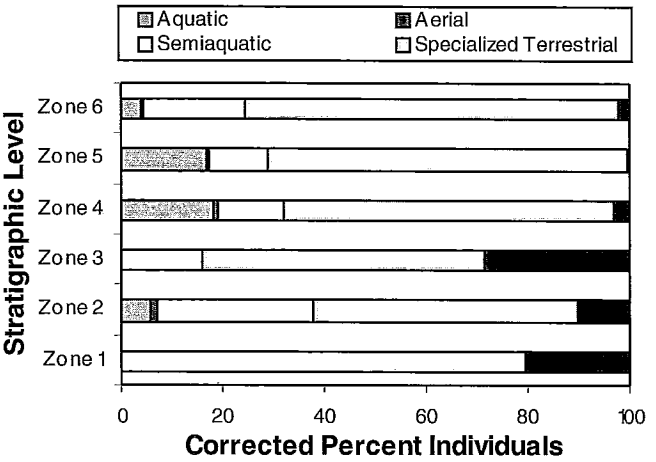

FIGURE 49. Relative abundance (in corrected percent individuals) of Morrison Formation vertebrates in Locomotion/Habitat guilds by stratigraphic level.

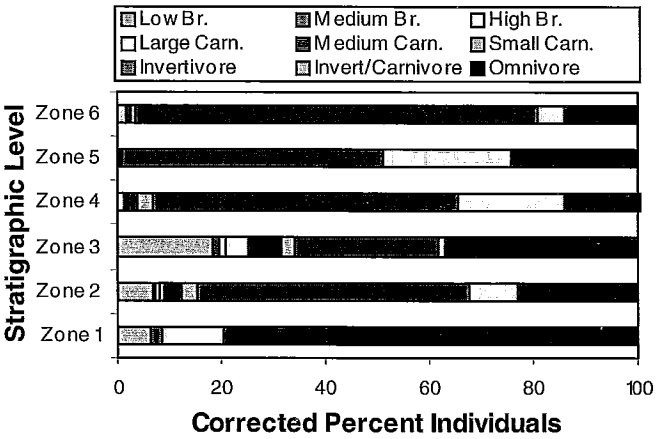

FIGURE 50. Relative abundance (in corrected percent individuals) of Morrison Formation vertebrates in Feeding Mode guilds by stratigraphic level.

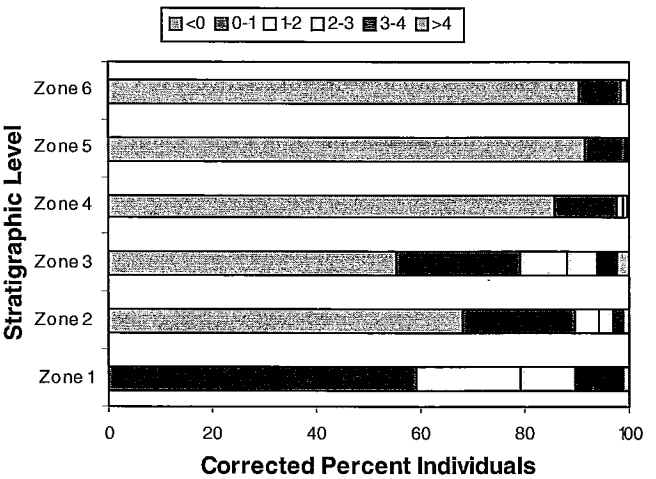

FIGURE 51. Relative abundance (in corrected percent individuals) of Morrison Formation vertebrates in weight categories by stratigraphic level. Weight category legend in Log10 kg.

23.8% observed; 11.6–12.6% expected), and Zones 5 and 6 have slightly lower than expected percentages (8.0–8.3% observed; ~15.7% expected). Zone 4 is close to its expected value. Zone 3 has

only 52 known specimens, so its corrected percentages may be less reliable than the others, but Zone 2 has close to a similar number of specimens as Zone 6 and demonstrates a different relative abundance of size classes. Zone 5 has nearly three times as many specimens as Zone 4 but has a similar distribution of size classes, so the differences between Zones 2 and 3, on the one hand, and Zones 4 through 6, on the other, may indicate a real shift toward greater abundances of very small animals and reduced abundances of larger animals around the Zone 3-Zone 4 contact. This contact is within the lower part of the Brushy Basin Member and corresponds to the clay change boundary identified by Peterson and Turner (1993). The cause of the apparent shift in body size is difficult to assess, even if it is real, but it should be noted that there are fewer or at least smaller microvertebrate localities in Zones 2 and 3 than in the upper levels of the formation. This may be a chance artifact of taphonomic or collecting patterns so far, or it may be a result of there truly being fewer small animals lower in the formation. The diversity within the size classes does not seem to change to the same degree as the relative abundances. If the size shift is real, environmental conditions may have had some effect and may be related to the cause of the clay change as well.

One possible cause of the apparent size-class relative abundance change, as mentioned above, is the presence of several large microverebrate quarries in the upper part of the formation. Specifically, these are the Fruita Paleontological Area in Zone 4, Quarry 9 in Zone 5, and the Rainbow Park sites in Zone 6. In order to determine what effect these might have had on the samples, the specimen counts were tallied by size class and the percentages calculated. These counts were not corrected in the manner the general counts were, as it appeared from the taphonomy of the sites and from the numbers of microvertebrates preserved that there was little bias against smaller animals. Figure 52 compares the counts from Quarry 9 to the corrected overall percents from Zones 2 and 5 (including Quarry 9). The apparent shift is recognizable here, as the percent of the Zone 2 sample in the <1 kg category is lower, and the percent in the 1–10 kg category is higher than those respective percentages from Zone 5. But, notice that the respective percentages of the uncorrected sample from Quarry 9 are very close to those of Zone 2. This suggests that: 1) the addition of non-Quarry 9 material to the Zone 5 count probably inflated and distorted the relative abundances; 2) the correction of Quarry 9 specimen counts was probably unnecessary and, combined with other specimens, even further distorted the abundances; and 3) Quarry 9 itself may be a good representative of the general relative abundances from its stratigraphic level and paleoenvironment. So the apparent shift of relative abundances of size classes may be an artifact of taphonomy and the way the data were analyzed.

Figure 53 compares the corrected percentages of Zone 2 to the uncorrected percentages of the Fruita Paleontological Area (Zone 4), Quarry 9 (Zone 5), and Rainbow Park (Zone 6). Here it appears that there is little difference between the distribution of Zone 2 and the Fruita Paleontological Area, again arguing against a size shift. Quarry 9 is a bit different with a greater percentage of 1–10 kg animals and very few above that, but Rainbow Park demonstrates an increase in the <1 kg category percentage and a roughly even percentage in all classes above that. The shift appears to be significant for Rainbow Park versus the others in the <1 kg (high) and 1–10 kg (low) categories ($X^2 = 16.9$, cv = 7.8, df = 3). This would seem to indicate that if there were a shift in abundance of size classes, it may occur near the very top of the formation and not near the clay change. Finally, in a test of the individual sites against their respective stratigraphic levels and against Zone 2 (Fig. 54), the Zone bar graphs are similar to each other in Zones 4 through 6 and these are different from Zone 2, but the

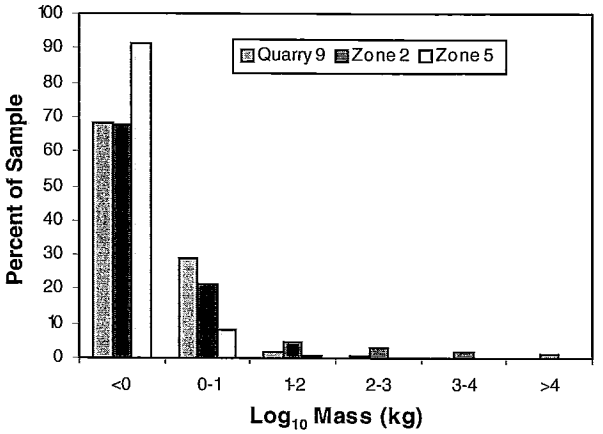

FIGURE 52. Comparison of the abundances in different mass categories, showing the similarity of an uncorrected count of Reed's Quarry 9 (Como Bluff) to the adjusted total samples from Zones 2 and 5. Quarry 9 sample percent is a number of identified specimens count and the other two samples are corrected percent individuals.

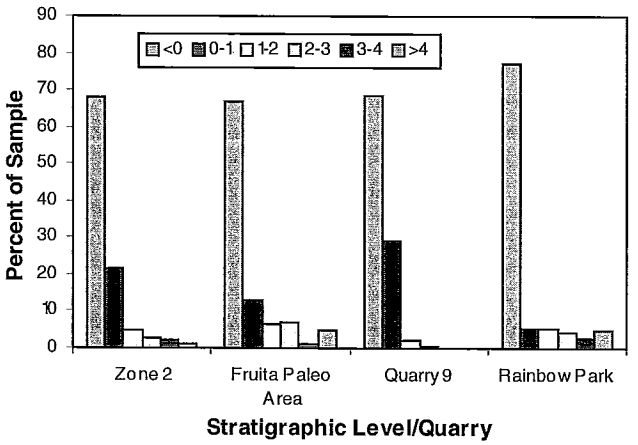

FIGURE 53. Comparison of the abundances in different mass categories of stratigraphic Zone 2 and three microvertebrate localities. Legend of weight categories is in Log_{10} kg.

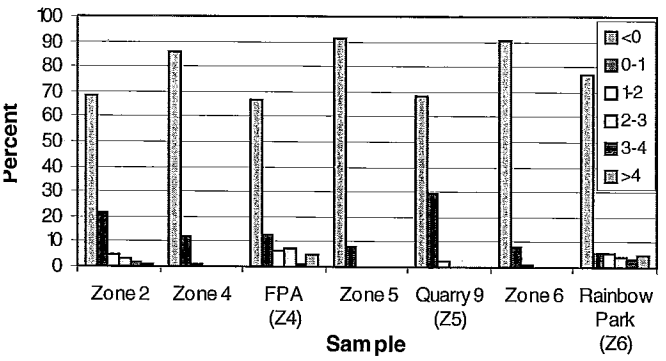

FIGURE 54. Comparison of the abundances in different mass categories of some stratigraphic Zones and representative microvertebrate quarries from each. Stratigraphic Zone samples are corrected percent individual counts; quarry samples are number of identified specimen counts. Legend of weight categories is in Log_{10} kg.

individual quarries demonstrate that Fruita is similar to Zone 2, Quarry 9 is different from both in having many <1 kg and 1–10 kg animals and little else but is otherwise similar, and Rainbow Park is different from all in having more <1 kg animals. This combined evidence suggests that some change in the relative abun-

dances of different size classes toward greater numbers of smaller animals did occur but that it was closer to the top of the formation and not as far down as suggested in Figure 51.

The relative abundances of the Feeding Mode guilds (Fig. 55) and size classes (Fig. 56) in different paleoenvironments indicate much the same pattern as the diversity graphs. Preservation of each category is largely dependent on taphonomic effects, and few associations of abundances of categories and paleoenvironments are discernable.

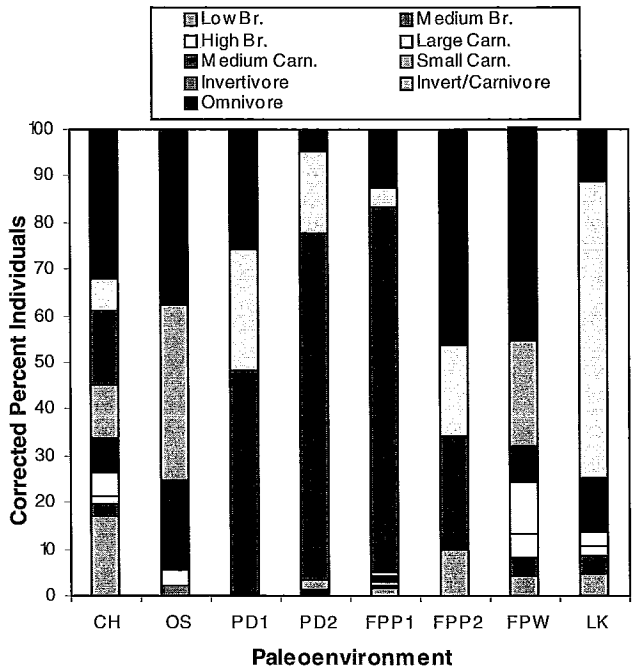

FIGURE 55. Relative abundances of Morrison Formation vertebrates in Feeding Mode guilds by each paleoenvironment. Paleoenvironmental abbreviations as in Table 2.

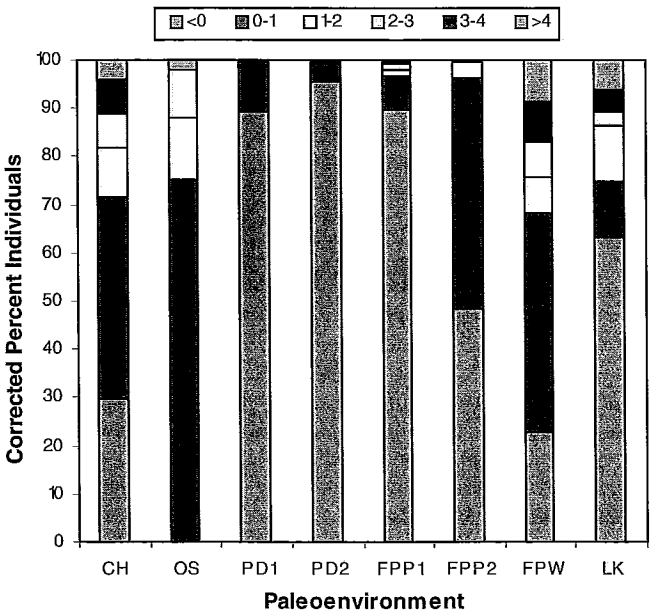

FIGURE 56. Relative abundances of Morrison Formation vertebrates in each weight category by paleoenvironment. Paleoenvironmental abbreviations as in Table 2.

Biomass Trends

The distribution of corrected biomass percentages for different Feeding Mode guilds at different stratigraphic levels (Fig. 57) indicates that the vertebrate biomass of the Morrison at all times was dominated by High, Medium, and Low Browsers. Analysis of these guilds from Zones 2 through 6 indicates significant variation, despite the apparent consistency ($X^2 = 22.8$, cv = 15.5, df = 8). The main differences are higher than expected percentages of Low Browsers in Zone 2 (23.5% observed; 14.6% expected) and higher than expected High Browser percentages (50.0% observed; 35.7% expected) and lower than expected percentages of Medium Browsers (29.0% observed; 42.0% expected) in Zone 6. Zone 3 through Zone 5 have very consistent percentages of Feeding Modes. The shift in Zone 6 may be largely due to the presence of several specimens of the very large sauropod *Camarasaurus supremus* at one locality at Garden Park in Colorado. The greater biomass of Low Browsers in Zone 2 may be real or may be due to the abundance of the herbivorous dinosaur genera *Stegosaurus* and *Camptosaurus* at one site (Reed's Quarry 13) at Como Bluff in Wyoming. In general, it would appear that the biomass percentages of Feeding Mode guilds in the Morrison Formation were constant throughout the time of deposition, a period of up to seven million years.

Predator/Prey Ratios

Bakker (1980) used predator/prey ratios of dinosaurs from various formations to suggest high metabolic rates for dinosaurs. In the same volume, Farlow (1980) cautioned against direct use of these ratios as indicators of dinosaur physiology, for various reasons. The ratios are compared here as characteristics of the Morrison paleocommunity. The method used is similar to that employed by Bakker (1980) except that the relative abundances of taxa are corrected based on mass using the technique of Russell (in Coe et al., 1987). The number of juveniles of each taxon was relatively low and for each was in proportion to the relative abundance of the taxon; thus, all counts were based on adult weight. As in Bakker's investigation, the carnivorous taxa are considered potential prey as well, and the predator/prey ratio is simply the percentage of the total biomass contributed by the predators. All Morrison Formation vertebrate taxa were included in the total biomass, and only taxa that fed almost exclusively on other vertebrates were included in the predator percentage calculation (i.e. Large, Medium, and Small Carnivore Feeding Mode guilds - theropods, semiaquatic and terrestrial crocodilians, snakes);

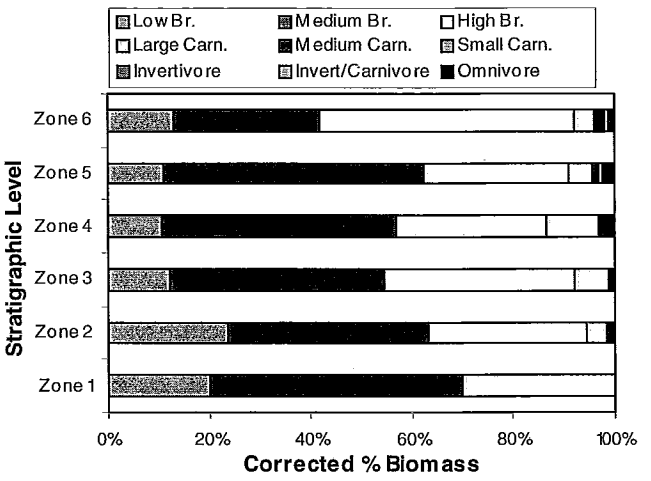

FIGURE 57. Corrected percent biomass accounted for by each Morrison Formation vertebrate Feeding Mode guild by stratigraphic level, showing the domination of biomass by browsing herbivores.

Invertivore taxa, though predatory, did not feed mainly on vertebrates but likely were consumed by small theropods and other carnivores and thus were included in the overall biomass but not that of the predators. Since little is known specifically about the diets of carnivorous taxa in the Morrison, I compared overall numbers and did not plot the ratios of specific taxa against specific prey by predator mass.

This technique assumes, as Bakker (1980) noted, that the populations were steady and that the number of skeletons produced and preserved was roughly equivalent to the secondary productivity of the taxa. The correction method should account for the preservational bias against the original numbers of skeletons available. Farlow (1993) noted some of the other assumptions involved in the use of predator/prey ratios. Most important among these is that one assumes that all productivity of the prey species is consumed by the carnivores, but in that study Farlow was mainly concerned with large tyrannosaur-size theropods and had to discount smaller theropods. In this case, because we are including all theropods as well as non-dinosaurian predators, the assumption is a bit less problematic, though it is probably impossible that all biomass was being consumed by predators. Other assumptions that Farlow (1993) noted were relatively even distributions of predator and prey species and that prey species distribution densities were fairly high. Another factor here is the assumption that a given carnivorous taxon consumed relatively even and high amounts of the productivity of all of its utilized prey taxa. Farlow (1980) noted that a more even consumption of prey species would result in lower predator/prey ratios than if the predator concentrated more on one of the species. Thus, highly diverse, potentially specialized communities of predators could appear to have lower predator/prey biomass ratios than they had in reality.

The predator/prey biomass ratio for the Morrison Formation as a whole is 8.6%. The values range from 5.1–11.9% at various stratigraphic levels (Table 7). Comparisons of dinosaur-only predator/prey biomass demonstrates a range from 4.4–11.0%, with an average of 6.44%.

Bakker's (1980) predator/prey ratios for dinosaur communities range from <1% to just over 5%, very similar to modern and fossil mammal communities. Béland and Russell (1980) felt that taphonomic variations would distort fossil assemblages to a degree that ecological conclusions could not be drawn from such data. Russell himself (Coe et al., 1987; Russell, 1989) later employed the work of Behrensmeyer et al. (1979) to try to offset some of the taphonomic bias, and Bakker's (1980) investigation found no significant taphonomic effect on Cenozoic mammal fossil community ratios. Given the differences between the Morrison and any community from the Cenozoic, the data used here were corrected, and hopefully, some characteristics of the paleocommunity are still reasonably represented.

The overall predator/prey ratio in the Morrison (8.6%) is above any of Bakker's ratios, but is still at the top end of the fossil mammal range. The range of variation within the Morrison Formation by stratigraphic level is from the top end of Bakker's dinosaur range up to the lower end of the vertebrate ectotherm range. If these ratios were to mean anything about the physiology of dinosaurs, it is important to remember that the predator/prey biomass for the Morrison includes taxa that are generally agreed to have been ectothermic (crocodilians). This fact would increase the ratio of endothermic dinosaurian predators. On the other hand, the crocodilians and medium and small theropods combined only account for 1.3% of the Morrison biomass, so the adjusted formation-wide ratio of large theropods (about 7.3%) would still be higher than most other dinosaur ratios graphed by Bakker (1980). The Morrison ratio and range may indicate the "intermediate"

TABLE 7. Calculated predator/prey ratios for the Morrison Formation.

Overall Morrison Formation Predator/Prey Biomass Ratio:		8.6%
Ratios By Stratigraphic Level:	Zone 6	6.0%
	Zone 5	5.6%
	Zone 4	11.9%
	Zone 3	8.0%
	Zone 2	5.1%
	Zone 1	—

dinosaurian metabolism proposed by some, but it is interesting that it is more within the upper range of mammalian ratios than in the lower range of that of ectotherms. It is important to emphasize, however, the previously-mentioned assumptions involved and the fact that the possible metabolic implications only directly relate to the predators and would not necessarily suggest that all prey species had similar physiologies.

The Morrison Formation predator/prey ratio is not at unusually high or low levels, despite the fact that some of the prey species had adult weights of 20–40 times that of the largest common predator and that many of the predator species were in fact relatively small, regardless of common belief about the great size of all dinosaurs. Of the ten theropod taxa in the Morrison Formation, just three are more than 1000 kg and two of those are very rare; another four theropods are less than 100 kg.

Based on a calculation of Farlow (1993), predicted population densities of the Morrison theropods range from 5.11 animals/km^2 for *Ornitholestes* to 0.022 for *Saurophaganax*. The most common large theropod, *Allosaurus*, has a predicted density of 0.061 animals/km^2. Adjusting for the different relative abundances of the theropod taxa (*Allosaurus* alone accounts for ~74% of the total number of theropod specimens known from the formation), the greatest densities of animals occurred among *Coelurus*, *Ornitholestes*, and *Allosaurus*. By measure of biomass, *Allosaurus* still dominated the predator population. The 8.6% ratio of predator-to-prey biomass was thus a result of moderate numbers but a large biomass of *Allosaurus* and large numbers but a low amount of biomass contributed by small theropods like *Ornitholestes* and *Coelurus*. This may suggest that *Allosaurus* was the main predator on a variety of medium-sized dinosaurian prey, and considering its relative abundance, *Allosaurus* was probably less selective and less specialized in its feeding than other large theropods like *Torvosaurus* and *Ceratosaurus*. (The biomass input of these latter taxa, though small, may then have led to slightly underestimated predator/prey ratios, as they probably consumed a far lesser percentage of most of their potential prey's individual productivities than would have more generalized, more abundant predators.) The significantly larger teeth and relative rarity of *Ceratosaurus* and *Torvosaurus* may suggest that these theropods were more specialized on slightly larger prey, perhaps including juvenile and sub-adult sauropods, than was *Allosaurus*. If *Allosaurus* was indeed a common, generalized predator that fed on a wide variety of dinosaurian taxa, this may have allowed a higher diversity of more specialized theropod taxa than would have been present if *Allosaurus* were more restricted in its feeding and less dominant numerically.

Small theropods, meanwhile, probably concentrated on smaller, often non-dinosaurian prey, and the total biomasses of both predatory small theropods and small non-dinosaurian prey had little effect on the predator/prey ratios. The small theropods could have fed on a variety of small vertebrates and been less specialized in feeding because there was a great diversity and number of smaller animals, particularly mammals.

Dinosaurs – Relative Abundance Trends

The corrected percentages of individuals were also analyzed with dinosaurs and other vertebrates separately, because there was probably enough taphonomic difference between the preservation of the two that comparing each separately would be justified. The dinosaurs-only corrected percent individuals of Feeding Mode guilds (Fig. 58) demonstrate an unusually high number of Large Carnivores in Zone 4 and a high number of Low Browsers in Zone 6. The increase of Low Browsers may be related to a possible increase in abundance of small ornithopods near the top of the formation, but it is very difficult to explain the increase in Large Theropods just at the Zone 4 level. Otherwise, abundances appear relatively consistent through the formation.

The abundance distributions of dinosaurian weight classes (Fig. 59) reflect attributes of the Feeding Mode abundance distributions. The higher than expected abundance of Low Browsers in Zone 6 is reflected in high abundance of 1–10 kg dinosaurs in Figure 59. Otherwise the distributions are fairly consistent from one level to another throughout the formation.

The abundances of different dinosaur groups by stratigraphic level (Fig. 60) indicate consistency in Zones 2, 3, and 5. Zones 4 and 6 show some significant variation (X^2 = 30.7, cv = 12.6, df = 6). The comparison included large and small theropods and ornithopods from Zone 2 through Zone 5. The percentage of large theropods in Zone 4 is again unusually high, and the percentage of ornithopods a bit low. The abundance of ornithopods relative to other dinosaurs is particularly high in Zone 6.

Except for the variations in Zones 4 and 6, the overall pattern is very consistent, with ornithopods comprising ~50–60% of the dinosaur assemblage, followed in abundance by large and small theropods and then sauropods, stegosaurs, and ankylosaurs. The apparent abundance of ornithopod dinosaurs in the Morrison Formation contrasts with Wing and Tiffney's (1987) assertion that small herbivores were rare before the Campanian. Diversity of these animals indeed was relatively low, but they were not particularly rare (see *Camptosaurus* and "small ornithopods" in Fig. 26). The abundance of ornithopods relative to other herbivorous taxa indicates that the diet of theropods must have included a relatively high percentage of ornithopods as prey compared to juvenile sauropods and other herbivores. Also, the rather high abundance of theropods generally (~20–25% of the dinosaur assemblage), relative to herbivorous taxa, suggests that theropods were either bradymetabolic nearly to the same degree as many modern reptiles or that many theropods fed also on non-dinosaurian prey. I prefer the latter explanation because many of the theropod taxa from the Morrison Formation were probably small enough to have fed mainly on mammals, lizards, and other non-dinosaurian vertebrate prey, and because the evidence for at least intermediate levels of metabolism in several dinosaur lineages is compelling.

Dinosaurs – Biomass Trends

The corrected biomass of the dinosaur assemblage by stratigraphic level and Feeding Mode guild (Fig. 61) suggests striking consistency in Zones 3 through 5. Even Zones 2 and 6 are fairly similar overall, though High Browsers increase in biomass percent in Zone 6 and Low Browsers are sightly higher than expected in biomass in Zone 2. Only Low, Medium, and High Browsers, and Large Carnivores contribute any significant biomass to the dinosaurian assemblage. The medium- and high-browsing sauropods constitute approximately 80% of the biomass, and this would seem to support Bakker's (1978) statement that sauropods and stegosaurs together account for nearly 95% of the preserved biomass. As with previous graphs, the zone-to-zone percentages

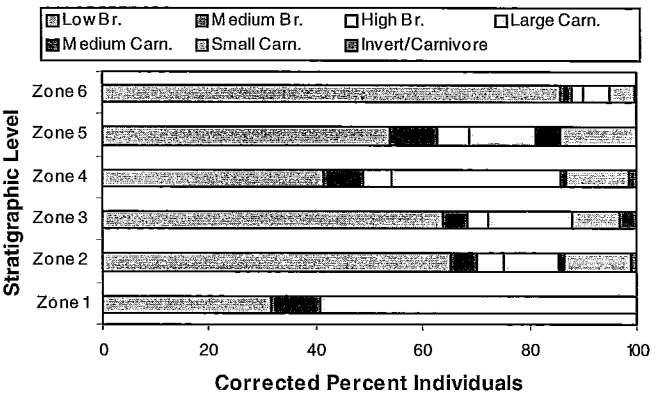

FIGURE 58. Corrected percent individuals of Morrison Formation dinosaur taxa in each Feeding Mode guild by stratigraphic level.

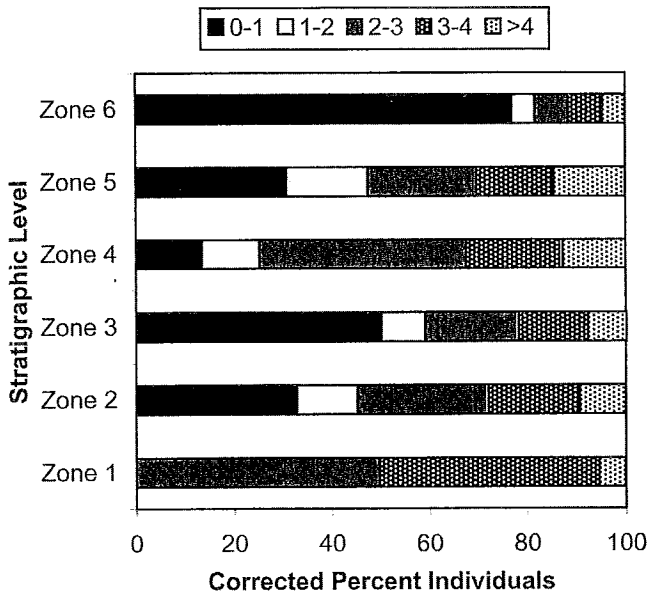

FIGURE 59. Corrected percent individuals of Morrison Formation dinosaurs in each weight category by stratigraphic level. Legend of weight categories in Log_{10} kg.

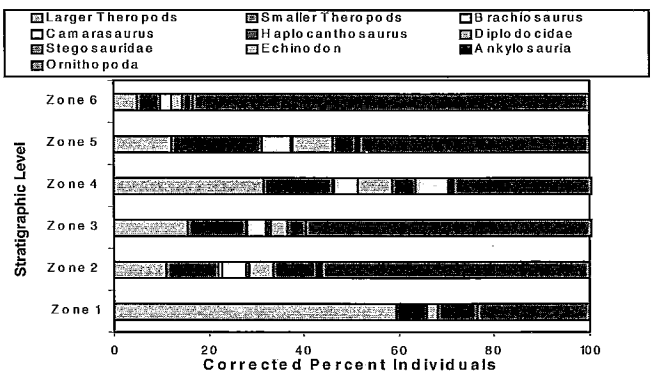

FIGURE 60. Corrected percent individuals of Morrison Formation dinosaur groups by stratigraphic level, showing numeric abundance of the Ornithopoda.

may be significantly steady from Zone 2 through Zone 6 if not for Reed's Quarry 13 (which may have increased the biomass of Low Browsers in Zone 2 with its great abundance of *Stegosaurus* and *Camptosaurus*) and if not for the large *Camarasaurus supremus* skeletons at Garden Park (which alone may have increased the High Browser biomass in Zone 6). In fact, *Camarasaurus* is the only

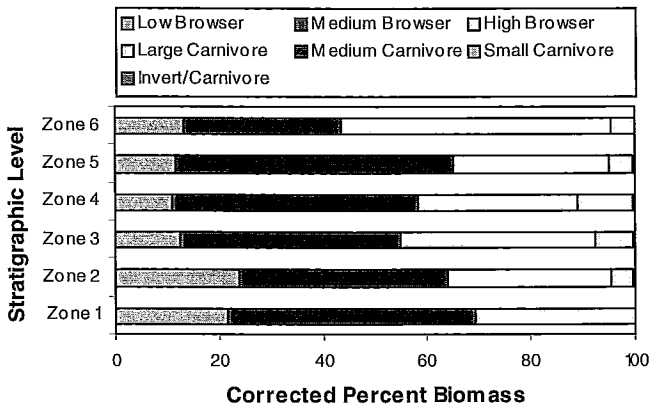

FIGURE 61. Corrected percent biomass of Morrison Formation dinosaurs in Feeding Mode guilds by stratigraphic level.

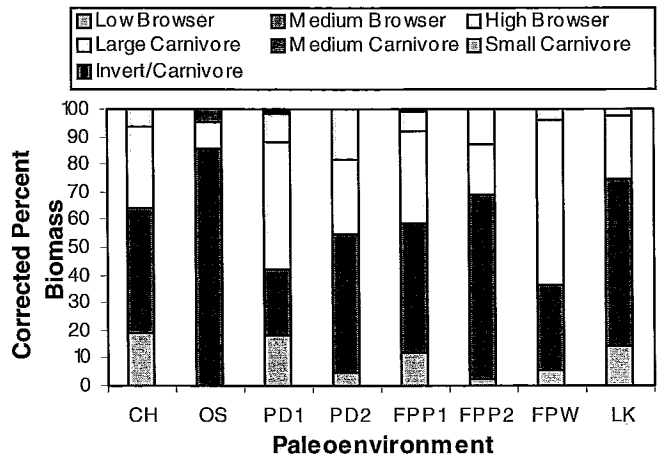

FIGURE 62. Corrected percent biomass of Morrison Formation dinosaurs in Feeding Mode guilds by paleoenvironment. Paleoenvironmental abbreviations as in Table 2.

known High Browser from Zone 6, and *C. supremus*, at ~47,000 kg, was probably the heaviest vertebrate of Morrison times. So, most likely, the dinosaurian biomass distribution of Feeding Mode guilds was very consistent for a period of perhaps 3–4 my from Zone 2 through the top of the formation.

Corrected biomass distributions of Feeding Mode guilds of dinosaur taxa by paleoenvironment (Fig. 62) show very similar percentages to Figure 61 in that High, Medium, and Low Browsers, and Large Carnivores, to one degree or another, dominate the biomass across all paleoenvironments. This indicates the presence of most taxa in a wide variety of environments as noticed by Dodson et al. (1980). High Browsers dominate the biomass to an unusual degree in Well Drained Floodplain paleoenvironments, but this too may be an artifact of the concentration of *Camarasaurus supremus* at Cope's quarries at Garden Park. The low abundance of microvertebrates in the Well Drained Floodplains seen in other graphs is probably a result of the taphonomic bias of the destruction of small skeletons before burial and not necessarily that no small animals lived in these areas. The relatively high biomass abundance of High and Medium Browsers may be a result of these being among the few kinds of animals whose skeletons could survive the pre-burial environment out on the drier parts of the floodplain or perhaps could be a result of real preference relative to other taxa for these areas. One puzzling aspect of Figure 62 is the relatively high biomass percentage of High Browsers and low percentage of Medium Browsers in the Type 1 Pond Deposits. The cause of this pattern is difficult to determine.

Non-Dinosaurian Vertebrates – Relative Abundance Trends

Because the dinosaur taxa were examined separately, the same was done for non-dinosaurian taxa. The corrected percent individuals of different Locomotion/Habitat categories (Fig. 63) indicates similar trends to previous graphs in that Semiaquatic taxa are fairly abundant in Zone 2. Analysis of the Aquatic, Semiaquatic, and Specialized Terrestrial categories from Zone 2 through Zone 6 indicates that Semiaquatic taxa are significantly more common than expected in Zone 2 and slightly lower than expected in Zones 4 and 5 and that the percentage of Aquatic taxa is lower than expected in Zone 6 ($X^2 = 31.5$, cv = 15.5, df = 8). The Semiaquatic taxa comprised 33.7% of the non-dinosaurian population in Zone 2 versus an expected population percentage of 19.4%. The Specialized Terrestrial taxa dominated the non-dinosaurian population numerically, and the population percentage increased steadily from Zone 2 through Zone 6 but was always close to the expected values.

The comparison of non-dinosaurian vertebrate Feeding Mode guilds by Morrison stratigraphic level (Fig. 64) demonstrates consistency from Zone 2 through Zones 4 and 5 ($X^2 = 7.85$, cv = 9.49, df = 4), comparing only those guilds that have high enough expected values (Invertivores, Invert/Carnivores, and Omnivores). Zones 1 and 3 were not included because they only contain six and ten non-dinosaurian specimens, respectively. Most likely, the relative abundances of Feeding Mode guilds within the Morrison were steady up through Zone 5. Zone 6 shows a significant increase in relative abundance of the Invertivores and a decrease in the Invertivore/Carnivores. This may be a real change in relative abundances of guilds or it may be a result of there being large numbers of lizard and sphenodontian specimens from the Rainbow Park sites at Dinosaur National Monument. A number of mammal specimens are known from several Zone 6 sites, but perhaps not enough to balance out the numbers of small reptiles. Another possible cause of the high abundance of Invertivores relative to Invert/Carnivores is that there is just one specimen of triconodont (along with fish one the most numerous taxa of the latter guild) known from Zone 6. Probably this, along with the pocket of small reptiles from Rainbow Park, is what has caused the apparent changes in abundances of the two guilds, and at some point when there are larger collections from Zone 6 the relative percentages could look much more similar to the lower stratigraphic levels. This again would indicate apparent stability in the relative abundances of Feeding Mode guilds during most of Morrison Formation deposition. Medium Carnivores (crocodilians) seem to be numerically less significant members of the community.

Non-Dinosaurian Vertebrates – Biomass Trends

The corrected biomass percentages of non-dinosaurian Locomotion/Habitat categories by stratigraphic level (Fig. 65) indicate that Semiaquatic taxa (mainly turtles and crocodilians) dominate the biomass. The numbers of other categories were too low to allow any real analysis, but the Semiaquatic dominance seems to be consistent at almost all levels. The low biomass representation of the Specialized Terrestrial category in Zones 2 and 3 is probably a result of small collections from these levels and is not necessarily that significant.

The corrected biomass of Feeding Mode guilds (Fig. 66) demonstrates that the biomass is dominated mainly by Medium Carnivores (crocodilians), Omnivores (turtles and multituberculates), and to some degree Invertivore/Carnivores (fish and triconodonts). There is consistency between the testable stratigraphic levels except Zone 5. Analysis of Zones 2, 4, and 6 (Zones 1 and 3 have too few specimens) indicates the variation in biom-

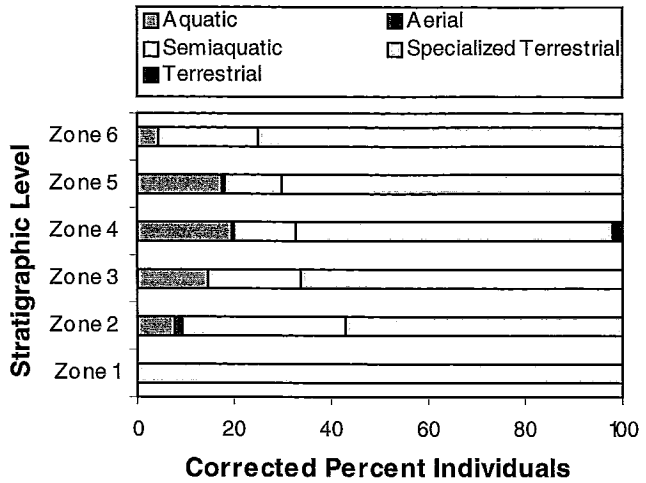

FIGURE 63. Corrected percent individuals of non-dinosaurian taxa in Locomotion/Habitat guilds by stratigraphic level.

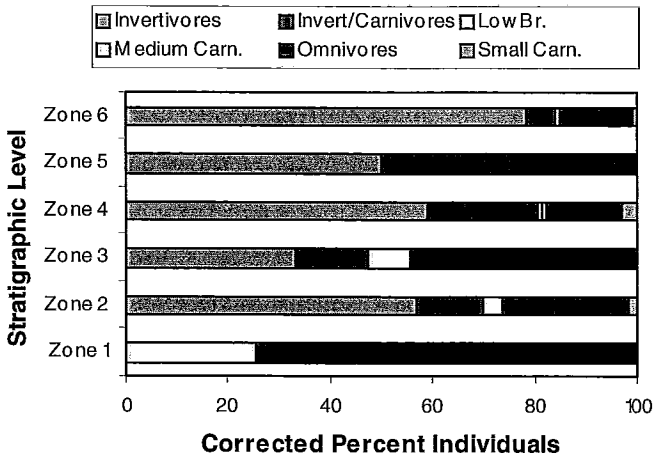

FIGURE 64. Corrected percent individuals of non-dinosaurian taxa in Feeding Mode guilds by stratigraphic level.

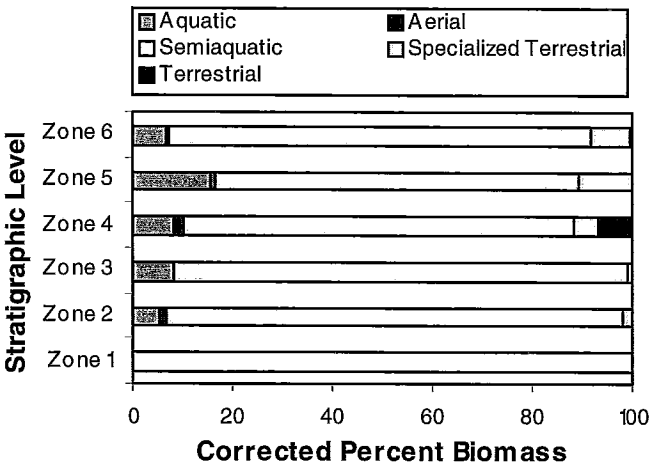

FIGURE 65. Corrected percent biomass of non-dinosaurian taxa in Locomotion/Habitat guilds by stratigraphic level.

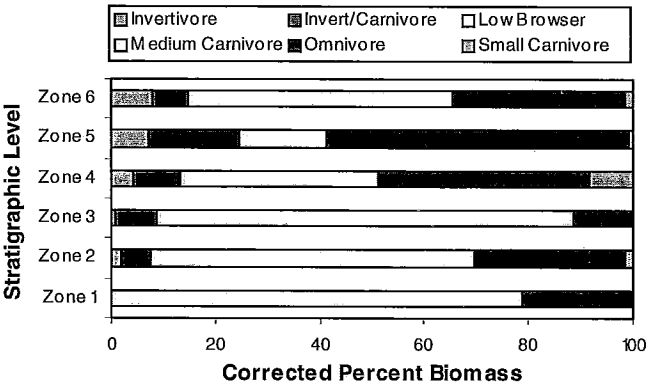

FIGURE 66. Corrected percent biomass of non-dinosaurian taxa in Feeding Mode guilds by stratigraphic level.

ass by Feeding Mode is not significant at the 0.05 level ($X^2 = 12.3$, cv = 12.6, df = 6). Inclusion of Zone 5, however, indicates significant increases in biomass of Invertivore/Carnivores and Omnivores relative to other guilds ($X^2 = 51.6$, cv = 16.9, df = 9). Quarry 9 may have some effect on the Zone 5 percentages, but it does not seem to have an inordinately high number of turtles or multituberculates among Omnivores. Medium Carnivores (crocodilians) are particularly low in biomass percentage at this level as well. This is difficult to explain, but I suspect that this all is a result of the Quarry 9 sample and that the percentages are in reality unvaried throughout the formation.

The corrected biomass by paleoenvironment and Feeding Mode (Fig. 67) indicates Omnivore and Medium Carnivore dominance of the biomass in most environments. Medium Carnivores appear less dominant in Pond and Poorly Drained Floodplain environments where there is greater preservation of Invertivore, Omnivore, and Invert/Carnivore taxa. Turtles may have in fact been more common and crocodilians less common in ponds than in streams. The restriction of Invertivores to Pond and Poorly Drained Floodplain paleoenvironments is likely taphonomic and not habitat-significant.

An additional comparison done was of just the Terrestrial and Specialized Terrestrial non-dinosaurian taxa. The corrected percentages of individuals of Feeding Mode guilds of terrestrial non-dinosaurian taxa from different stratigraphic levels (Fig. 68) demonstrates some consistency from testable levels, but the numbers of Omnivores from Zones 4 and 5 are lower and higher than expected, respectively ($X^2 = 16.5$, cv = 5.99, df = 2). The significance here is again difficult to assess, but most likely Quarry 9 has a substantial effect on the numbers from Zone 5. The low numbers for Omnivores in Zone 4 are probably a result of taphonomic characteristics as well. There does not seem to be much difference between the diversities of these groups between the levels. The key here is that Invertivores still dominate numerically as they did with the Aquatic and Semiaquatic taxa included, so the previous analyses probably were relatively accurate.

Possible Food Web

Figure 69 presents a simplified hypothetical food web for Morrison Formation vertebrates. Presumably, herbivorous and carnivorous terrestrial invertebrates (mostly arthropods) served as the main food for most mammals, amphibians, and lizards. Feeding on these vertebrates were predators such as the small theropods (*Ornitholestes*, *Coelurus*, *Koparion*), terrestrial crocodilians, and the one known snake. Herbivores included the stegosaurs, ankylosaurs, ornithopods, diplodocids, *Haplocanthosaurus*, *Brachiosaurus*, and *Camarasaurus*. These were prey for the next level of larger theropods such as *Allosaurus*, *Ceratosaurus*, *Torvosaurus*, *Marshosaurus*, and *Stokesosaurus*. Aquatic invertebrates (arthropods and molluscs) and plants served as the main food of turtles, actinopterygian fish, *Cteniogenys*, and lungfish; these were fed on by crocodilians. There was probably a fair amount of overlap in

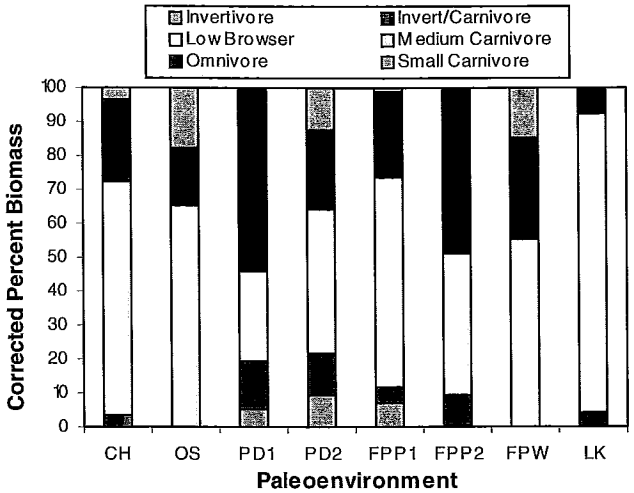

FIGURE 67. Corrected percent biomass of non-dinosaurian vertebrates in Feeding Mode guilds by paleoenvironment. Paleoenvironmental abbreviations as in Table 2.

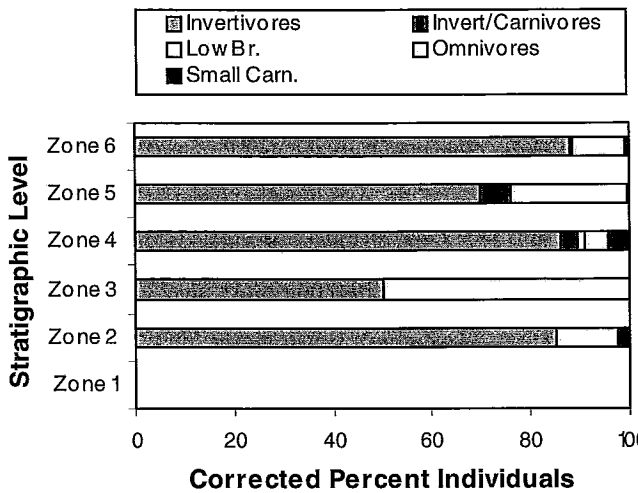

FIGURE 68. Corrected percent individuals of non-dinosaurian terrestrial taxa in each Feeding Mode guild by stratigraphic level.

diets as well. *Cteniogenys* probably fed on insects and small fish, pterosaurs on fish and small vertebrates when possible, crocodilians on small dinosaurs when they were near the ponds and rivers, and turtles on amphibians and small vertebrates. Docodonts and multituberculates probably fed on seeds and other plant material as well as insects, triconodonts on very small vertebrates as well as insects, and larger theropods on smaller. Both aquatic and terrestrial environments have about four trophic levels.

The web contains a minimum of four trophic levels, but the number of links can be as high as seven. For example, large theropods such as *Allosaurus* can feed at level 3 when feeding on herbivorous dinosaurs, but seven levels exist between plants, herbivorous invertebrates, insectivorous small vertebrates, and various-sized predators. Various studies of food webs suggest that communities with shorter, more connected webs are more stable that those with many trophic levels and fewer prey species per predator, although stability studies of complex systems suggest that above a certain number of species increasing connectance actually reduces stability (Rosenzweig, 1995; Gotteli and Graves, 1996). In this case, stability means independence of species populations to variations in other species; for example, highly connected

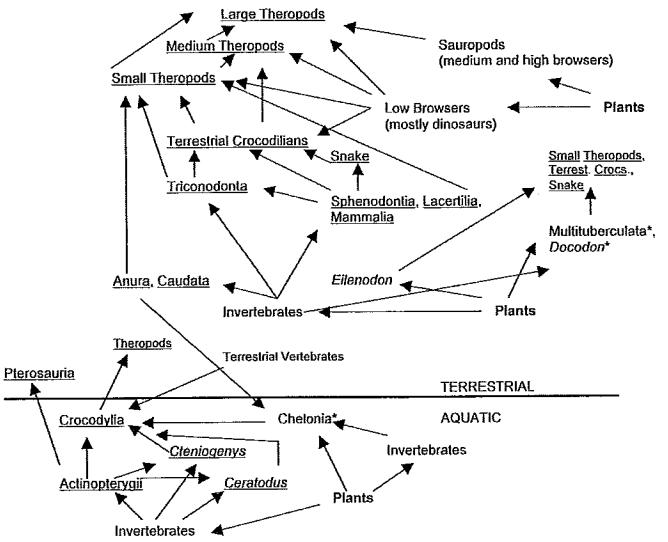

FIGURE 69. Hypothetical food web for Morrison Formation vertebrate taxa. Arrows indicate energy flow. Producers are in bold, primary consumers in regular text (unless italicized), and consumers at the secondary or higher levels are underlined. Omnivores feed from more than one major level and are marked with asterisks.

food webs allow predators to concentrate on other prey when one prey population drops. Thus, fluctuations of one species do not necessarily affect all others. The Morrison Formation web seems to be fairly highly connected and to have an average number of trophic levels. Predatory species have a variety of possible prey species available. The main difference separating this web from those of modern studies is that there is no way to directly observe diet for an ancient species and thus most features of the web are highly speculative.

CONCLUSIONS

Analysis of the data compiled for this study has allowed some preliminary conclusions to be drawn regarding the vertebrate paleocommunity structure and paleoecological history of the time of deposition of the Morrison Formation:

1) The Morrison Formation paleocommunity was different from any modern community and most ancient ones in having a relatively high abundance and diversity of very large vertebrate animals.

2) Given the occurrence of similar and even shared genera between the Morrison Formation and other Late Jurassic paleofaunas around the world, it is likely that the vertebrate paleocommunities of these other regions also were very different from modern communities and that some of the patterns apparent in the Morrison Formation record may be recognized in other deposits.

3) The adult weight class distribution of prey species in the Morrison Formation is unusual in having a high diversity of large to very large animals, as well as a very high diversity of small animals (<10 kg), but very few in mid-ranges (10–500 kg). Predators, on the other hand, are more evenly distributed among size classes and are most diverse among mid to large size classes (10–100 kg and 1–10 tonnes). The paucity of prey species in the 10–500 kg adult weight category may have been a result of competitive pressure from juveniles of larger dinosaur species, as well as possibly selective pressure from predators in the mid to large sizes.

4) Relative abundances of small non-dinosaurian vertebrates and dinosaurs less than 10 kg may have increased somewhat in

the upper part of the formation (Zone 6).

5) The overall diversity of Morrison Formation vertebrates was relatively high and fairly consistent throughout most of the time of deposition of the formation.

6) The diversity of Locomotion/Habitat guilds was consistent through time as well, at least above the clay change in the middle of the formation.

7) The diversity of Feeding Mode guilds was relatively evenly distributed and consistent through time.

8) Fluvial channel paleoenvironments preserve the most even diversities of vertebrate sizes; Type 1 Poorly Drained Floodplains preserve relatively even diversities but are highest in small vertebrates; Pond deposits produce the most diverse collections and are particularly high in small vertebrate diversity; and Well Drained Floodplains preserve relatively higher diversities of larger animals.

9) There is no apparent significant variation in biogeographic distributions of most vertebrate taxa.

10) Among the Mammalia, multituberculates occur at the greatest number of localities (12), dryolestids are most common in having the highest ratio of number of specimens/number of localities (19.2), and *Docodon* is often the most common single genus at any one locality at which it is found.

11) Although small vertebrate animals were probably numerically by far the most common vertebrates in the Morrison Formation, the vertebrate biomass appears to have been dominated by large herbivores to an even greater degree than modern megaherbivore communities. This biomass dominance may have suppressed small reptile biomass through habitat modification and by possibly increasing the diversity and abundance of predators that may have also fed on smaller reptiles. Habitat modification may also have been beneficial to smaller herbivores.

12) Microvertebrate localities such as the Fruita Paleontological Area and Quarry 9 may provide good examples of original paleocommunities, as they preserve different size classes in relative abundances similar to the corrected abundances of multisite samples from single stratigraphic levels. If these sites do provide reasonable examples, this would also seem to indicate that the relative abundances of size classes are consistent throughout Morrison time, except for the possible increase in small animal relative abundance in Zone 6.

13) The Morrison Formation predator/prey biomass ratio was ~8.6%, and most of the predator biomass consisted of *Allosaurus*; other less common large theropod taxa may have been more specialized carnivores; and the diversity of smaller predators probably consisted of taxa that concentrated on the variety of small vertebrates.

14) The theropod dinosaur *Allosaurus* outnumbers all other theropods combined more than 2 to 1 across stratigraphic levels and paleoenvironments and is present in all geographic areas of Morrison Formation exposure. It was apparently a very important ecological component of the Morrison dinosaur community.

15) Approximately 50% of the individuals in dinosaur populations during Morrison deposition were ornithopods. These dinosaurs thus were important ecologically both as numerically common low browsers and as potential prey for theropods.

16) The consistency of relative abundances of Feeding Mode guilds between stratigraphic levels in the Morrison Formation is maintained even when non-dinosaurian taxa are analyzed separately from dinosaurs.

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APPENDIX

This section details the main data used in this study from fossil vertebrate localities. Abbreviations are as follows:

Main Collection Method:
QU = Quarrying operations
SU = Surface collection
SW = Screenwashing

Data Collection:
PO = Personal observation of museum and field specimens, museum collection records and data
RE = References such as published papers and unpublished reports
VS = Field visitations of quarries and field areas
PC = Personal Communication

Paleoenvironment:
As in Table 2

Counting Methods:
MNI = Minimum Number of Individuals
NIS = Number of Identified Specimens

Stratigraphic Levels:
Zones 1–6, as in Figure 6.

Notes:
A = Adult
J = Juvenile
H = Hatchling (very young juvenile)

ARIZONA

Navajo County

Piñon Locality

Main Collection Method:	SU
Data Collection:	PC, RE
Stratigraphic Level:	-
Paleoenvironment:	-
Geographic Tiers:	South, West

Taxa	MNI
Apatosaurus	1

COLORADO

Delta County

Young Locality

Main Collection Method:	SU, QU
Data Collection:	RE, VS
Stratigraphic Level:	Zone 1
Paleoenvironment:	FPW
Geographic Tiers:	Middle, West

Taxa	MNI
Crocodilia indet. (Terres.)	1
Chelonia	1
Theropoda	1

El Paso County

Garden of the Gods

Main Collection Method:	QU
Data Collection:	PO, VS, RE
Stratigraphic Level:	-
Paleoenvironment:	-
Geographic Tiers:	Middle, Central

Taxa	MNI
Camptosaurus	1

Fremont County

Cleveland Quarry

Main Collection Method:	QU
Data Collection:	PO, VS, RE
Stratigraphic Level:	Zone 1
Paleoenvironment:	OS
Geographic Tiers:	South, Central

Taxa	MNI
Haplocanthosaurus	1
Eutretauranosuchus	1
Glyptops	1
Theropoda	1

Cleveland II

Main Collection Method:	QU
Data Collection:	PO
Stratigraphic Level:	-
Paleoenvironment:	-
Geographic Tiers:	South, Central

Taxa	MNI
Haplocanthosaurus	1

Cope's Nipple

Main Collection Method:	QU
Data Collection:	PO, VS, RE
Stratigraphic Level:	Zone 6
Paleoenvironment:	FPW
Geographic Tiers:	South, Central

Taxa	MNI
Camarasaurus supremus	6
Allosaurus	2
Apatosaurus	1
Diplodocus (*Amphicoelias*)	1
Stegosaurus	1
Goniopholis	1
Glyptops	1

Cope Quarry 8 (The Fort)

Main Collection Method:	QU
Data Collection:	RE
Stratigraphic Level:	Zone 6
Paleoenvironment:	-
Geographic Tiers:	South, Central

Taxa	MNI
Camarasaurus supremus	1

Cope Quarry 12

Main Collection Method:	QU
Data Collection:	PO, RE
Stratigraphic Level:	Zone 6
Paleoenvironment:	-
Geographic Tiers:	South, Central

Taxa	MNI
Diplodocus (*Amphicoelias*)	1

Cope's Mystery Localities

Main Collection Method:	QU
Data Collection:	RE
Stratigraphic Level:	-
Paleoenvironment:	-
Geographic Tiers:	South, Central

Taxa	MNI
Glyptops	2

Camarasaurus	2
Apatosaurus	1
Camptosaurus	1
Stegosaurus	1

DeWeese Quarry

Main Collection Method:	QU
Data Collection:	PO, VS
Stratigraphic Level:	Zone 4
Paleoenvironment:	FPP1
Geographic Tiers:	South, Central

Taxa	MNI
Diplodocus	1
Glyptops	1
Theropoda	1
Crocodylia	1

Egg Gulch

Main Collection Method:	SU, QU
Data Collection:	PO, VS
Stratigraphic Level:	Zone 3
Paleoenvironment:	FPP1, LK
Geographic Tiers:	South, Central

Taxa	MNI	Notes
Dryosaurus	1	FPP1
Crocodylia	1	LK

Eric's Tooth

Main Collection Method:	SU
Data Collection:	PO, VS
Stratigraphic Level:	-
Paleoenvironment:	-
Geographic Tiers:	South, Central

Taxa	MNI
Allosaurus	1
Glyptops	1
Crocodylia	1

Felch Quarry 2

Main Collection Method:	QU
Data Collection:	RE, VS
Stratigraphic Level:	Zone 3
Paleoenvironment:	CH
Geographic Tiers:	South, Central

Taxa	MNI
Allosaurus	1
Camarasaurus	1
Diplodocus	1

Garden Park General

Main Collection Method:-
Data Collection:PO
Stratigraphic Level:-
Paleoenvironment:-, CH
Geographic Tiers:South, Central

Taxa	MNI	Notes
Allosaurus	1	
Glyptops	2	
Stegosaurus	1	J
Othnielia	1	
Camarasaurus	1	CH

Green Acres General

Main Collection Method:	SU
Data Collection:	PO, VS
Stratigraphic Level:	-
Paleoenvironment:	-
Geographic Tiers:	South, Central

Taxa	NIS
Glyptops	11
Ornithopoda	2
Theropoda	1
Crocodylia	1
Eilenodon	1

Greg's Bone

Main Collection Method:	-
Data Collection:	RE
Stratigraphic Level:	-
Paleoenvironment:	-
Geographic Tiers:	South, Central

Taxa	MNI
Stegosaurus	1

Jennings and Johnsonn

Main Collection Method:	SU
Data Collection:	PO, VS, RE
Stratigraphic Level:	Zone 6
Paleoenvironment:	OS
Geographic Tiers:	South, Central

Taxa	MNI
Hallopus	1

Kenny's *Stegosaurus*

Main Collection Method:	-
Data Collection:	RE
Stratigraphic Level:	Zone 3
Paleoenvironment:	-
Geographic Tiers:	South, Central

Taxa	MNI
Stegosaurus	1

Kessler Quarry

Main Collection Method:	QU
Data Collection:	PO
Stratigraphic Level:	Zone 2
Paleoenvironment:	FPP1
Geographic Tiers:	South, Central

Taxa	MNI
Stegosaurus	1
Allosaurus	1
Glyptops	1
Goniopholis	1
Ornithopoda	1

Lindsey Quarry

Main Collection Method:	QU
Data Collection:	PO, RE
Stratigraphic Level:	Zone 4
Paleoenvironment:	PD2
Geographic Tiers:	South, Central

Taxa	NIS	Notes
Actinopterygii	2	
Anura	1	
Glyptops	11	
Opisthias	1	
Crocodylia	1	
Allosaurus	3	2A, 1J
Diplodocus	1	
Camarasaurus	2	1A, 1J

Lucas's Site

Main Collection Method:	QU
Data Collection:	RE, PO